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ESTUDIO DE LA EVOLUCION DE LA TRICOBOTRIOTAXIA A TRAVES DEL DESARROLLO POSTEMBRIONARIO DE *THERIDION RUFIPES* (ARANEAE, THERIDIIDAE)¹

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ABSTRACT

Trichobothriotaxic evolution was studied through the postembryonic development of *Theridion rufipes*. It was found that this species belongs to the plesiomorphic pattern (Lehtinen 1980) and only presents basal growth. The number of trichobothria on the tibia of the male palp is three and on the female palp is five. The total number of trichobothria on specimens of different sexes is similar because the same number of molts is necessary for reaching adult stage, being six trichobothria on the tibia of leg IV for both sexes. On the tibia of leg I the number of trichobothria is five in males and six in females. The individual variation between right side and left or between specimens of different sexes is not significant.

EXTRACTO

En el presente trabajo se estudió la evolución de la tricobotriotaxia a través del desarrollo postembrionario de *Theridion rufipes*. Se demostró que esta especie pertenece al patrón plesiomórfico (Lehtinen 1980); posee únicamente crecimiento basal; el número de tricobotrias de las tibias de los palpos en machos y hembras es de tres y cinco respectivamente; el número total de tricobotrias es semejante en ambos sexos porque igual número de mudas es necesario para alcanzar el estado adulto (en la tibia de la pata IV es igual a seis para ambos sexos y en la tibia de la pata I es igual a cinco en los machos y seis en las hembras); la variación individual entre el lado derecho e izquierdo o entre ejemplares de distinto sexo no es significativa.

INTRODUCCION

Las únicas investigaciones existentes sobre el estudio tricobotriotáxico de arañas de la familia Theridiidae (González 1980, 1984) se refieren a especies del género *Latrodectus* Walckenaer 1805.

En el presente trabajo se llevó a cabo el estudio de la evolución de las tricobotrias a lo largo del desarrollo postembrionario de *Theridion rufipes*, determinando: (1) el momento de aparición, (2) la distribución en los artejos de los apéndices estudiados, (3) el número total por artejo, (4) el modo de aparición, (5) la variación individual entre los apéndices del lado derecho e izquierdo de un individuo en un estado del desarrollo y entre ejemplares de distinto sexo.

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Para tal fin se efectuó: (1) el seguimiento de la evolución de los órganos mecanorreceptores en las tibias de palpo, pata I y pata IV y en el metatarso de pata I y pata IV durante el desarrollo en ambos sexos, (2) la comparación de varias series procedentes de una misma madre, (3) la comparación de los artejos de los apéndices opuestos de un mismo par en un mismo ejemplar, (4) la comparación de las tablas tricobotrióticas de machos y hembras en un mismo estado.

MATERIAL Y METODOS

Para realizar las investigaciones se utilizaron las exuvias sucesivas de machos y de hembras y los ejemplares adultos de ambos sexos. Las observaciones se efectuaron a partir de la cuarta exuvia por ser ésta la primera que presenta tricobotrias, (la cuarta exuvia es la primera que se produce fuera de la ooteca, contando como muda uno el desprendimiento de la cutícula embrional que arrastra consigo al diente de eclosión).

Todo el material empleado fue criado en el laboratorio a partir de los desoves de arañas colectadas en el campo. Las condiciones de laboratorio y los métodos de cría fueron explicados en una publicación anterior (González 1979). Las observaciones se realizaron en seco, sobre lotes de 20 exuvias de cada estado.

Se empleó para la identificación de las tricobotrias la nomenclatura espacio-temporal propuesta por Emerit y Bonaric (1975).

RESULTADOS OBTENIDOS

Theridion rufipes, como todas las arañas de la familia Theridiidae, responde al patrón plesiomórfico o grupo 1 (Lehtinen 1980). Es decir que presenta todas las tricobotrias en la zona dorsal del artejo con una única tricobotria metatarsal subdistal y dos líneas paralelas tibiales. No se observan tricobotrias en tarso y fémur.

Modo de aparición.—En esta especie se observó un crecimiento basal. La primera tricobotria (tricobotria promotora) de una serie surge en la zona proximal del territorio respectivo, luego en mudas sucesivas, se aleja hacia la zona distal del mismo, para dar lugar a la aparición de nuevas tricobotrias, las que se reconocen fácilmente por ser más cortas y de cúpulas más pequeñas. No se ha observado el crecimiento intercalar citado por Emerit y Bonaric (1975) y observado para *Latrodectus mirabilis* (Holmberg 1876) (González 1980).

Tricobotrias tibiales.—En los apéndices estudiados se reconocieron dos territorios: (1) proximal (T) desde la mitad del artejo hacia la articulación tibia-patela, (2) distal (S) desde la mitad del artejo hacia la articulación tibia-metatarso.

En cada territorio se hallan comprendidos dos campos: anterior (A) y posterior (P) teniendo en cuenta la línea media dorsal del artejo.

En la nomenclatura empleada, el número anterior a las letras que identifican los territorios y sus campos corresponden al estado del desarrollo en que aparece la tricobotria y el número posterior, a la filiación de la misma.

Palpos: Los ejemplares adultos, machos y hembras, poseen tres y cinco tricobotrias respectivamente. Esta característica ha sido observada para las

Tabla 1.—Evolución tricobotriotáxica tibial en machos.

	Palpo		Pata I		Pata IV	
	P	A	P	A	P	A
S	4-PS1		5-PS1 6-PS2		4-PS1 5-PS2	7-AS1
T	6-PT1	5-AT1	4-PT1	4-AT1 5-AT2	5-PT1	4-AT1 5-AT2

especies de la familia Theridiidae tratadas en trabajos anteriores (González 1980, 1984). No obstante el orden de aparición de los órganos mecanorreceptores y su distribución, difieren entre *Theridion rufipes* y las especies del género *Latrodectus* estudiadas.

En los machos de *Theridion rufipes* aparece en el estado cuatro la tricobotria PS1, en el estado cinco la AT1 y en el estado seis la PT1.

En las hembras se observó en el estado cuatro la PS1 y en estado cinco la AT1, esto concuerda con la evolución dada en los machos. En el estado seis de las hembras no surge ninguna tricobotria nueva. En el siguiente estado aparecen juntas la AT2 y la PT1, completándose el número de cinco tricobotrias, con la aparición de la PT2 en el estado adulto.

En las Tablas 1 y 2 y en la Figura 1 se halla representada la evolución, distribución y número de las tricobotrias para las tibias de los palpos de machos y de hembras separadamente.

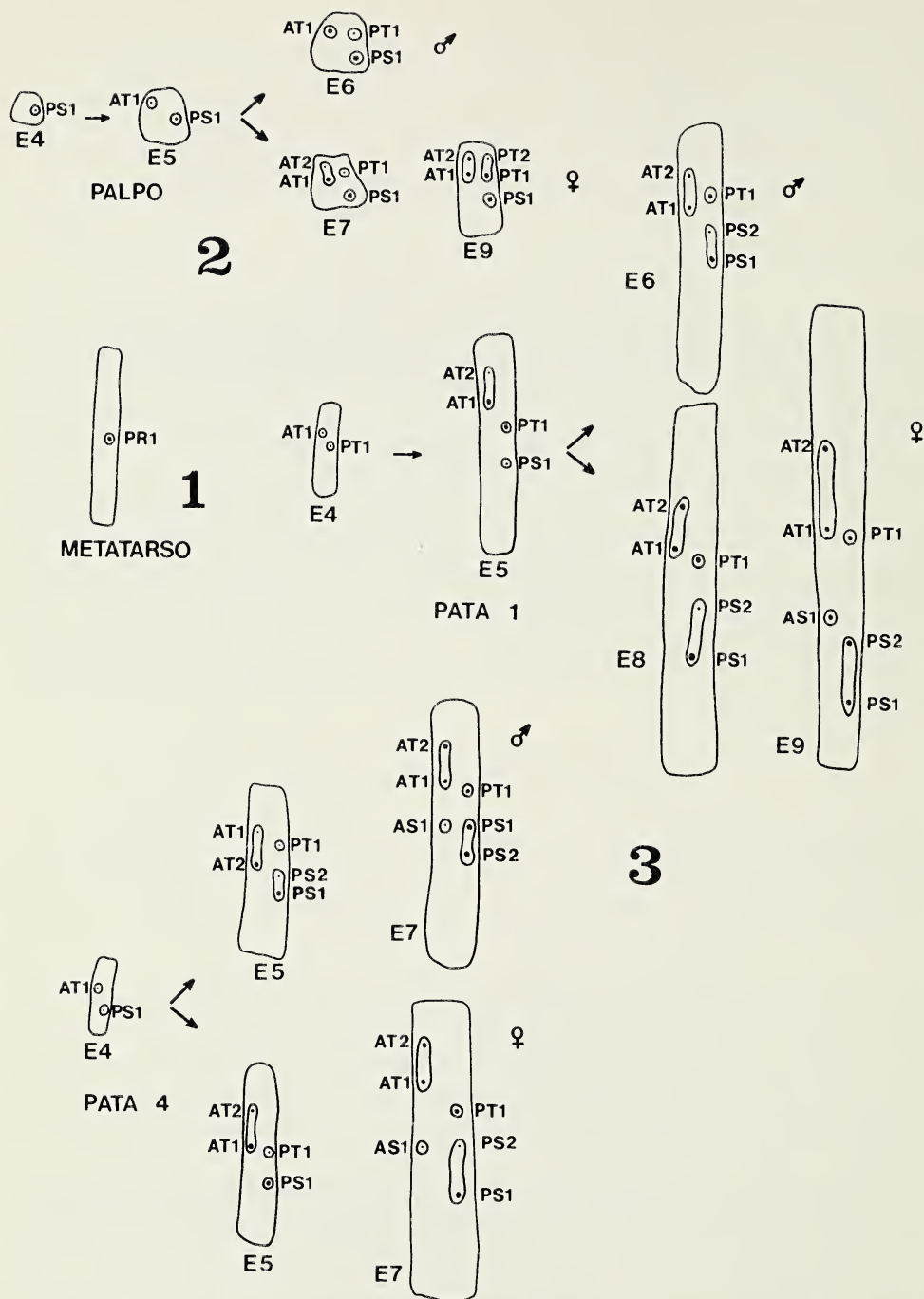
Pata I y Pata IV: En la pata I, en el estado cuatro, surgen dos tricobotrias en los machos y en las hembras, la AT1 y la PT1; en el estado cinco, coincide para ambos sexos, la aparición de la AT2 y la PS1. A partir de aquí, difiere el orden de aparición. En los machos se observa una nueva tricobotria en el estado seis, la PS2, la cual aparece en las hembras en el estado ocho. La tricobotria AS1 surge en las hembras en el estado adulto, no existiendo en los machos ninguna tricobotria en el campo anterior del territorio distal.

En la pata IV, machos y hembras presentan el mismo número de tricobotrias (seis) y la misma distribución, pero difieren en la secuencia de aparición. En el estado cuatro aparecen la AT1 y la PS1 en los dos sexos. En el estado cinco, en los machos, se observa la PT1, la AT2 y la PS2, mientras que en las hembras en este estado sólo aparecen la PT1 y la AT2. La PS2 surge en las hembras en el estado siete, junto con la AS1, la cual aparece en ese mismo estado en los machos.

Las Tablas 1 y 2 y las Figuras 2 y 3 muestran la evolución tricobotriotáxica y los mapas tricobotriales de machos y hembras para ambos apéndices. Del análisis

Tabla 2.—Evolución tricobotriotáxica tibial en hembras.

	Palpo		Pata I		Pata IV	
	P	A	P	A	P	A
S	4-PS1		5-PS1 8-PS2	9-AS1	4-PS1 7-PS2	7-AS1
T	7-PT1 9-PT2	5-AT1 7-AT2	4-PT1	4-AT1 5-AT2	5-PT1	4-AT1 5-AT2



Figuras 1-3.—Mapas tricobotriotaxómicos de *Theridion rufipes*: 1, metatarso de pata I; 2, tibia de palpo de machos y hembras; 3, tibia de pata I y pata IV de machos y hembras. E = estados del desarrollo.

de los mismos surge, que si bien el orden de aparición de las tricobotrias difiere entre machos y hembras, el número total de las mismas presenta escasas diferencias, lo que se debe, probablemente, a que ambos efectúan el mismo número de mudas para llegar al estado adulto.

Tabla 3.—Variación de la tricobotriotaxia tibial en función de los sexos. \bar{x} = promedio de tricobotrias de palpo + pata I + pata IV; S = desviación típica; n = número de individuos; Ex = estado del desarrollo.

Ex	Macho		Hembra		t
	n	$\bar{x} \pm S$	n	$\bar{x} \pm S$	
4	5	5.00 \pm 0	5	5.00 \pm 0	—
5	6	11.00 \pm 0.81	5	10.00 \pm 0.63	2.04
6	5	13.20 \pm 0.74	7	11.00 \pm 1.07	3.86
7	6	13.16 \pm 0.69	7	13.85 \pm 0.83	2.41
8	6	13.83 \pm 0.69	6	14.66 \pm 0.94	1.90
9	6	14.33 \pm 0.94	6	16.83 \pm 0.69	4.5

Tricobotrias metatarsales.—De las observaciones efectuadas surge la existencia de una tricobotria metatarsal sólo en la pata I. Esta se encuentra ubicada en el campo posterior (P) del territorio proximal (R). Aparece en la cuarta exuvia y permanece invariable a lo largo del desarrollo (Fig. 4, PR1).

Variación tricobotriotáxica.—Emerit y Bonaric (1975) se refieren a la variación tricobotriotáxica individual, como a la variación que puede existir respecto del número de tricobotrias entre los apéndices derecho e izquierdo del mismo par y del mismo individuo, y a la variación del número de tricobotrias entre ejemplares de distinto sexo, para un mismo estado del desarrollo. El poder utilizar la tricobotriotaxia para delimitar el estado del desarrollo al que pertenece un individuo, depende de la variabilidad de estos dos factores citados.

En la Tabla 3 se demuestra que las diferencias entre el número de tricobotrias de machos y hembras para un mismo estado, no es significativa para ningún porcentaje de probabilidad (test de Student). Podemos decir entonces que la tricobotriotaxia de *Theridion rufipes* no presenta diferencias significativas entre los sexos para determinar el estado del desarrollo de un ejemplar.

Tabla 4.—Variación de la tricobotriotaxia tibial entre el lado derecho e izquierdo de un mismo ejemplar. \bar{x} = promedio de tricobotrias de palpo + pata I + pata IV; S = desviación típica; n = número de individuos; Ex = estados del desarrollo.

Ex	Derecho		Izquierdo		<i>t</i>
	<i>n</i> y	$\bar{x} \pm S$ (y)	<i>n</i> y	$\bar{x} \pm S$ (y)	
MALES					
4	5	5.00 \pm 0	5	5.00 \pm 0	—
5	6	11.00 \pm 0.81	6	11.83 \pm 0.90	1.9
6	5	13.20 \pm 0.74	5	12.20 \pm 0.4	2.38
7	5	13.00 \pm 0.63	5	14.00 \pm 0.89	1.97
8	7	13.71 \pm 0.70	6	14.83 \pm 0.90	2.24
9	6	13.16 \pm 0.69	5	14.60 \pm 0.80	2.94
FEMALES					
4	5	5.00 \pm 0	5	5.00 \pm 0	—
5	5	10.00 \pm 0.63	6	10.83 \pm 0.69	2.0
6	7	11.00 \pm 1.07	6	10.00 \pm 0.82	1.8
7	7	13.85 \pm 0.83	7	13.00 \pm 0.75	2.02
8	6	14.66 \pm 0.94	6	15.60 \pm 0.47	2.09
9	6	16.83 \pm 0.69	5	17.60 \pm 0.49	1.95

En la Tabla 4 se compara los apéndices opuestos de un mismo ejemplar a través de su desarrollo. Las diferencias observadas no son significativas, ni para probabilidades del 95%, ni del 99% (test de Student), por lo que podemos tomar indistintamente los valores de derecha o izquierda de un individuo para los estudios tricobotriotáxicos y poder determinar así el estado del desarrollo de un individuo.

CONCLUSIONES

1—La especie *Theridion rufipes* responde al patrón plesiomórfico (Lehtinen 1980).

2—La tricobotria más antigua de una serie, aparece en la zona proximal del territorio y se va alejando hacia la zona distal del mismo, dando lugar a la aparición de tricobotrias nuevas (crecimiento basal).

3—Las tricobotrias nuevas se reconocen fácilmente por ser más cortas y de cúpulas más pequeñas.

4—El número de órganos mecanorreceptores tibiales de los palpos de los machos y de las hembras es de tres y cinco respectivamente, estableciéndose ésto, como una característica de la familia Theridiidae.

5—El número total de tricobotrias de los ejemplares adultos de distinto sexo es semejante, por realizar machos y hembras la misma cantidad de mudas para alcanzar el estado adulto.

6—La variación individual de los órganos mecanorreceptores que se puede presentar entre apéndices opuestos de un individuo en un estado dado del desarrollo o entre ejemplares de distintos sexos, no es significativa para *Theridion rufipes*, pudiéndose emplear la tricobotriotaxia para reconocer estadios.

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SPECIES OF SPIDERS (ARANEAE) ASSOCIATED WITH THE IMMATURE STAGES OF *MANTISPA PULCHELLA* (NEUROPTERA, MANTISPIDAE)

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ABSTRACT

Species of spiders associated with the immature stages of *Mantispa pulchella* (Banks) are presented for the first time. Twenty species in 15 genera from the families Philodromidae, Anyphaenidae, Oxyopidae, Thomisidae, and Salticidae harbored immature stages of *M. pulchella* in South Carolina. Some characteristics of the life history of *M. pulchella* are analyzed and compared with those of other North American species of Mantispinae.

The cosmopolitan family Mantispidae was recently divided into the subfamilies Symphrasinae, Drepanicinae, Calomantispinae, and Mantispinae (Lambkin 1986). Little is known about the life histories of the first three subfamilies. Several species of the Symphrasinae have been associated with nests of aculeate Hymenoptera as well as with pupae of Noctuidae and Scarabaeidae (Parker and Stange 1965), and one species of the Drepanicinae has been associated with a spider egg sac (Austin 1985). Natural history of the Calomantispinae remains unknown, although MacLeod and Redborg (1982) suggested, based on laboratory rearings, that larvae of the Symphrasinae and Calomantispinae were generalist predators of sedentary arthropod prey. In contrast, adult Mantispinae have been reared exclusively from spider egg sacs (Redborg and MacLeod 1985; Brushwein 1986).

Female mantispines are not known to oviposit either on spider egg sacs or on spiders, and instead deposit clutches of approximately 200 to 2000 stalked eggs on leaves, pieces of wood, and other objects (McKeown and Mincham 1948; LaSalle 1986; Rice 1986b). Following eclosion, larvae locate and gain access to spider eggs by using one or both of two general strategies. Larvae may either seek out and penetrate previously deposited egg sacs or board female spiders and enter egg sacs as they are being formed (Redborg and MacLeod 1985). Larvae feed on

spider eggs by piercing the chorion and draining the contents. Pupation occurs within the egg sac, and pharate adults exit both their own cocoons and the egg sacs before emerging from the pupal skin.

The mantispine *Mantispa pulchella* (Banks) has been recorded previously from Utah, southern Illinois, Georgia, North Carolina, and Panama (Banks 1912; Hughes-Schrader 1969; Redborg 1976; Hoffman and Hamilton 1988). Both Redborg and MacLeod (1985) and Brushwein (1986) reported the successful rearing of this species during studies on other species, but no further details were presented. The present paper records the presence of *M. pulchella* in South Carolina for the first time, documents spider associations, analyzes some characteristics of the life history of this species, and compares these characteristics with those of other North American Mantispinae.

METHODS

The majority of the immature stages of *M. pulchella* and associated spiders were collected by the authors from March 1986 through April 1988 in and around Clemson, Pickens County, South Carolina. Spiders and spider egg sacs of as many different taxa as could be collected visually were examined for the presence of mantispine immatures. In addition, the spider collection within the Clemson University Arthropod Collection (CUAC) was searched and eight first instar *M. pulchella* were located. Prior to the present study, the CUAC contained 29 families, 101 genera, and 162 species of spiders from South Carolina (Gaddy and Morse 1985). However, the collections made during the course of the present study, that of Brushwein (1986), and the identification of previously undetermined material encountered during examination of the CUAC have increased the collection to 32 families, 167 genera, and 290 species.

Four adult *M. pulchella* were collected in 1986 in an ultraviolet light trap run nightly from January 1984 to October 1986, and 52 additional adults were located in the CUAC. The latter specimens had been collected from the South Carolina counties of Barnwell, Dorchester, Florence, Oconee, Pickens, and York from 1956 to 1986.

Identity of the immature stages of *M. pulchella* was confirmed by the subsequent rearing of some ($n = 18$) to adults, using procedures detailed elsewhere (Brushwein 1986). Some juvenile spiders were also reared to maturity for species-level identifications. Spiders were identified both by the use of selected taxonomic references (Edwards 1958; Kaston 1973; Platnick 1974; Dondale and Redner 1976, 1978; and Roth 1985) and with the kind assistance of A. R. Brady, G. B. Edwards, J. H. Redner, and S. H. Roach. Voucher specimens of *M. pulchella* and associated spiders were deposited in the CUAC, Department of Entomology, Clemson University.

RESULTS

Spiders were each associated with a single immature *M. pulchella*. First instars of *M. pulchella* were found either wrapped dorsally over the pedicel and posterior edge of the carapace of spiders (Fig. 1) or inside spider egg sacs, whereas all other immature stages were found only inside egg sacs. Spiders with larvae on them

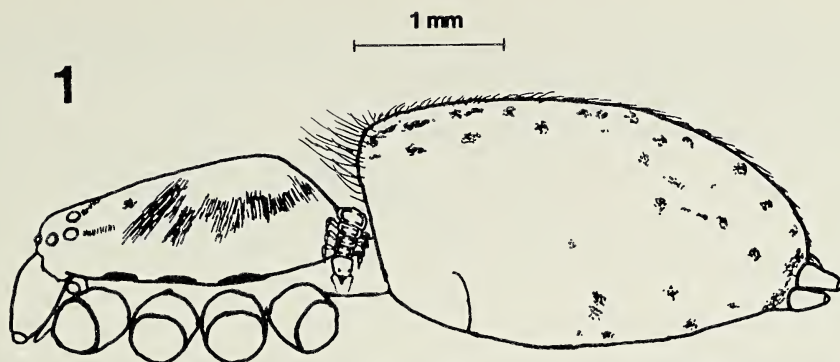


Figure 1.—Juvenile *Anyphaena* sp. with *Mantispa pulchella* larva in dorsal pedicel region, left lateral view. Palpal and leg segments distal to coxae omitted.

usually had discolored patches present on one or both sides of the pedicel; these patches were located ventrolaterally on the anterior portion of the pedicel or on the membranous area just below the posterior edge of the carapace. The dark patches were at the approximate location that larval mouthparts would come in contact with the spider integument.

Members of the family Anyphaenidae were the most commonly collected spiders associated with *M. pulchella* and comprised 65.7% ($n = 134$) of the records, followed by members of the Salticidae and Clubionidae at 19.4% and 10.4%, respectively (Table 1). The families Philodromidae, Oxyopidae, and Thomisidae combined for the remaining 4.5%. Larvae were associated with adults as well as with penultimate and earlier instars; and of the 87 spiders whose gender could be determined, 53 were males and 34 females. First instars of *M. pulchella* were found during all months, whereas all other immature stages were found only during May and June (Table 2). Adults were collected from May to September, with the majority collected during July.

DISCUSSION

The presence of *M. pulchella* larvae on spiders confirms that this species boards spiders to gain access to spider eggs. Five other North American species have been studied with respect to their strategies for gaining access to eggs. First instars of *Mantispa viridis* Walker located and entered previously deposited egg sacs and fed directly on the eggs within; larvae would not board spiders and therefore were termed obligate penetrators of egg sacs (Redborg and MacLeod 1985; Brushwein 1986). In contrast, first instars of *Climaciella brunnea* (Say) did not penetrate previously constructed egg sacs and would not feed on spider eggs unless larvae had previously been aboard spiders; larvae readily boarded spiders and were termed obligate spider boarders (Redborg and MacLeod 1983). Recent studies on neonate *M. pulchella* larvae have similarly failed to induce larvae to feed on spider eggs unless larvae had previously boarded spiders (Brushwein and Hoffman unpubl.). First instars of *Mantispa uhleri* Banks are facultative spider boarders because although they showed a strong preference for spider boarding over direct egg sac penetration, they could still penetrate egg sacs and develop without previously having boarded spiders (Redborg and MacLeod 1985). First

Table 1.—Spider taxa associated with immature stages of *Mantispa pulchella* in South Carolina. Numbers represent the number of collections of each taxon, broken down by developmental stage and gender. Superfamilies and families are arranged according to the taxonomic list presented by Shear (1986). (undet. = gender undetermined).

SUPERFAMILY	Developmental stage and gender					
	Adults		Juveniles			Egg sacs
	Male	Female	Male	Female	Undet.	
Family Species						
CLUBIONOIDEA						
Clubionidae						
<i>Clubiona maritima</i> L. Koch	0	1	0	0	0	0
<i>Clubiona obesa</i> Hentz	1	0	3	2	0	1
<i>Clubiona</i> sp., poss. <i>obesa</i>	0	0	1	0	2	0
<i>Clubionoides excepta</i> (L. Koch)	1	0	0	0	2	0
PHILODROMOIDEA						
Philodromidae						
<i>Philodromus imbecillus</i> Keyserling	0	0	0	0	0	1
<i>Philodromus vulgaris</i> (Hentz)	1	1	0	0	0	0
DICTYNOIDEA						
Anyphaenidae						
<i>Anyphaena fraterna</i> (Banks)	2	1	0	0	0	0
<i>Anyphaena pectorosa</i> L. Koch	0	1	1	1	0	0
<i>Anyphaena</i> sp., <i>pectorosa</i> group	0	0	21	7	23	0
<i>Aysa gracilis</i> (Hentz)	1	1	2	5	2	0
<i>Teudis mordax</i> (O. P.-Cambridge)	0	1	0	0	0	9
<i>Wulfila albus</i> (Hentz)	0	2	3	2	3	0
LYCOSOIDEA						
Oxyopidae						
<i>Oxyopes aglossus</i> Chamberlin	0	0	0	0	1	0
THOMISOIDEA						
Thomisidae						
<i>Misumenops asperatus</i> (Hentz)	0	0	1	1	0	0
SALTICOIDEA						
Salticidae						
<i>Eris marginata</i> (Walckenaer)	2	0	0	0	0	0
<i>Hentzia palmarum</i> (Hentz)	0	1	4	2	1	0
<i>Lyssomanes viridis</i> (Walckenaer)	0	0	0	0	1	0
<i>Maevia inclemens</i> (Walckenaer)	0	0	0	1	0	0
<i>Metacryba undata</i> (De Geer)	1	0	0	0	0	0
<i>Metaphidippus exiguus</i> (Banks)	7	3	0	0	0	0
<i>Metaphidippus galathea</i> (Walckenaer)	1	0	0	0	0	0
<i>Metaphidippus peckhamorum</i> Kaston	0	0	0	0	0	1
<i>Metaphidippus</i> sp.	0	0	0	1	0	0
Totals	17	12	36	22	35	12

instars of *Mantispa fuscicornis* Banks have been found on six species of spiders (Rice 1986b). In light of the current status of this species as a sibling species of *M. uhleri* (Hughes-Schrader 1979), *M. fuscicornis* larvae are probably also facultative boarders. Larvae of *Mantispa interrupta* Say have boarded and remained on a spider in the laboratory (Viets 1941), and recent studies indicate that larvae of this species are facultative spider boarders (Brushwein unpubl.). The behavior of *M. pulchella* larvae seems to be more similar to that of *C. brunnea* larvae than to that of other North American mantispine larvae, and therefore *M. pulchella* larvae are probably obligate boarders as well.

Table 2.—Number of *Mantispa pulchella* collected by month in South Carolina.

Month	<i>M. pulchella</i> Developmental stage				
	First	Second	Third	Pupa	Adult
January	17	0	0	0	0
February	4	0	0	0	0
March	6	0	0	0	0
April	15	0	0	0	0
May	6	1	0	0	3
June	2	3	1	6	2
July	1	0	0	0	46
August	12	0	0	0	3
September	13	0	0	0	2
October	12	0	0	0	0
November	15	0	0	0	0
December	20	0	0	0	0
Totals	123	4	1	6	56

Both the position occupied while on spiders and the number of larvae on each spider appear different for *M. pulchella* than for other species. *Mantispa pulchella* larvae were found wrapped over the dorsal pedicel region and only one larva was found per spider. In contrast, first instars of *M. uhleri* have been found wrapped either dorsally, ventrally, or laterally around the pedicel, inside the book lung slits, or, less commonly, on the membrane between the carapace and leg bases, on the legs, or around the spinnerets; some spiders had two or three larvae on them (Redborg and MacLeod 1985). Larvae of *M. fuscicornis* have been found wrapped ventrally around the pedicel, inside the book lung slits, or, less commonly, on the membrane between the carapace and leg bases or on a leg (Rice 1986b); it was not uncommon to find 2 or 3 larvae per spider (M. Rice pers. comm.). *Climaciella brunnea* larvae have only been found associated with the carapace and the membrane between the carapace and the leg bases; the presence of two larvae on a spider has been reported (Redborg and MacLeod 1983). The variability in the positions occupied by larvae of these other species affords multiple resting sites on a single spider and the large size of some of the hosts (e.g., the Lycosidae) allows for more than one larva in areas such as the pedicel region or carapace. In contrast, the combination of a single resting site and the relatively small size of the spiders associated with *M. pulchella* would seem to preclude multiple infestations.

First instar *M. pulchella* may sustain themselves by feeding on the hemolymph of the boarded spiders, thereby becoming true ectoparasites. Abdomens of larvae commonly were distended to the point that the abdominal banding pattern became diffuse. Similarly, first instars of *M. uhleri* on spiders appeared "plumper" than neonate larvae and were found to gain weight after boarding spiders (Redborg and MacLeod 1984). Also, the discolored patches on spiders boarded by *M. pulchella* appeared to be similar to those on spiders boarded by *M. uhleri*, which Redborg and MacLeod (1984) interpreted as evidence of larval feeding damage. If this interpretation is correct, then the occurrence of patches on both sides of a single pedicel indicates that *M. pulchella* larvae either occasionally reverse their orientation while on spiders or that the spider had been infested prior to the boarding by the current occupant.

The behavioral and morphological parameters of spiders that permit successful mantispine boardings are virtually unknown. However, the spiders associated with *M. pulchella* do share a few ecological and behavioral characteristics. All spiders were wanderers which do not build webs for prey capture and which are commonly found on foliage (Kaston 1978). In addition, members of the Anyphaenidae, Salticidae, and Clubionidae all construct tubular silken retreats for resting and molting in harborages such as curled leaves and beneath bark. Members of the Philodromidae, Oxyopidae, and Thomisidae do not. Therefore, while *M. pulchella* larvae appear to board primarily wandering spiders on foliage, spiders within retreats might be easier for larvae to locate or board than those not in retreats.

Five other North American mantispine species have been associated with spiders. Redborg and MacLeod (1985) found that *M. uhleri* larvae were associated with a wide variety of wandering spiders and attributed the lack of associations with web-building spiders to the inability of larvae to come into contact with spiders suspended in webs. Similarly, all spiders associated with *C. brunnea* larvae also were wanderers, namely the ground cursorial Lycosidae (LaSalle 1986; Redborg pers. comm.). *Mantispa fuscicornis* larvae were associated with both web-building and wandering spiders, but Rice (1986b) hypothesized that the presence of larvae on web-builders was due to the tendency of those particular species to retreat into the cracks and corners of a wooden shelter during the day and therefore became more accessible to larvae searching on that substrate. Larvae of *M. interrupta* have only been associated with three species of wandering spiders (Redborg and MacLeod 1985; Rice 1986a). In contrast, *M. viridis* larvae have been associated with a wide variety of both web-building and wandering spiders (Brushwein 1986). The above findings on other species coupled with the present data on *M. pulchella* suggest that mantispine species that use spider boarding to gain access to spider eggs generally will be associated with wandering spiders, whereas species whose larvae normally locate and penetrate previously deposited egg sacs will be associated with a wider diversity of both web-builders and wanderers.

The male to female ratio of 53 to 34 for spiders associated with *M. pulchella* seems in contrast to what might be expected, given that larvae board spiders in order to gain access to eggs. However, if the twelve infested egg sacs can be taken as an indication of larvae having boarded females prior to their oviposition, then the male to female ratio becomes essentially one to one (53 to 46). In any case, the male to female ratio of *M. pulchella* correlated well with results obtained by Redborg and MacLeod (1985) on *M. uhleri*, where the male to female ratio of spiders was 48 to 36 and where larvae boarded spiders of both genders with equal frequency in the laboratory.

The subsequent fate of *M. uhleri* larvae on male spiders was unclear because larvae failed to transfer from males to females when mating occurred. However, some larvae transferred from conspecific males to females when the male was cannibalized. Redborg and MacLeod (1985) argued that transfer of larvae during mating would require larvae to coordinate their transfer activities with the wide variety of courtship behaviors exhibited by the various spider species. In contrast, transfer of larvae during cannibalism required no such coordination and had the advantage of larval transfer from any spider to any other, regardless of sex, developmental stage, or species. The ability of larvae to transfer from one spider

species to another in this manner could therefore result in occasional transfers of larvae to spider species which for behavioral or morphological reasons would not normally be boarded by larvae of that particular mantispine species. Therefore, spider associations for a particular mantispine species could consist both of spider species which are normally boarded and of species which are not normally boarded but which acquired larvae via predation of infested spiders. Unfortunately, the extent to which the spider associations of *M. pulchella* reflect the latter category cannot be assessed at this time.

The presence of first instars of *M. pulchella* on spiders throughout the winter indicates that this species overwinters on spiders. Furthermore, the absence of any other developmental stages of *M. pulchella* during the winter months suggests that *M. pulchella* overwinters in South Carolina only as first instars on spiders. This species also may overwinter as eggs, but the lack of egg collections coupled with reports on the larval or pupal overwintering strategies of other species argues against this. Redborg and MacLeod (1985) concluded that *M. uhleri* overwintered in southern Illinois exclusively as first instars on spiders, and Brushwein (1986) concluded that *M. viridis* overwintered in northwestern South Carolina as either larvae or pupae within spider egg sacs.

The collection of second instar *M. pulchella* during May and June, of third instars and pupae during June, and of most adults during July indicates that this species is essentially univoltine in South Carolina. However, the possibility for more than one generation per year cannot be excluded. Additional generations could result from adult *M. pulchella* produced by spiders which bred early in the year subsequently producing larvae that board spider species destined to breed later in the year. Redborg and MacLeod (1985) and Brushwein (1986) discussed similar scenarios in relation to the seasonal cycles of *M. uhleri* and *M. viridis*, respectively. The spiders associated with both *M. uhleri* and *M. viridis* included species which bred during late summer and fall and, accordingly, an average of two generations per year was reported for *M. uhleri* in Illinois and a minimum of three generations were observed for *M. viridis* in South Carolina. However, no immature *M. pulchella* were found either on adult spiders or inside egg sacs from August until late December, indicating that the spider species used by *M. pulchella* all breed earlier in the year.

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PREDATORY BEHAVIOR OF THREE JAPANESE SPECIES OF *METLEUCAUGE* (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT

The predatory behavior of *Metleucauge kompirensis* (Boes. et Str.), *M. yunohamensis* (Boes. et Str.) and *Metleucauge* sp. was studied, and the natural prey of the former two species were collected from their webs. These species did not immobilize their prey by wrapping, but immobilized them only by biting. The lack of immobilization wrapping in *Metleucauge* can be explained by two different hypotheses: 1) *Metleucauge* remains in the primitive stage of the evolution of predatory behavior, or 2) the habit of immobilization wrapping has been lost, because *Metleucauge* captures weakly flying insects (mainly midges and mayflies) which can be immobilized without wrapping.

INTRODUCTION

It has been suggested that there are five stages in the evolution of predatory behavior in araneid spiders, judging mainly from whether immobilization wrapping is used or not (Robinson et al. 1969; Robinson 1975).

Robinson and his colleagues agreed with Eberhard (1967) that lack of immobilization wrapping is primitive, and immobilization wrapping is advanced. They supposed that immobilization wrapping was derived from post-immobilization wrapping (that is, the wrapping after immobilization by biting) at the capture site.

Alternatively, Levi (1985) suggested that the lack of immobilization wrapping in *Micrathena* and *Gasteracantha* is not a primitive character, but rather a secondary loss of immobilization wrapping.

Eberhard (1982) stated that immobilization wrapping evolved independently along three lines, Theridiosomatidae-Anapidae, Araneidae, and Tetragnathidae-Metinae. As examples of the spiders with immobilization wrapping in the Tetragnathidae-Metinae line, he listed *Dolichognanthe* spp., *Leucauge* spp., and *Chrysometa* spp. *Tetragnatha praedonia* also sometimes uses immobilization wrapping with large prey (Yoshida 1987). The predatory behavior in the Tetragnathidae-Metinae line has been studied only fragmentarily, and no species without attack wrapping has yet been found.

Levi (1980) included Tetragnathidae in the Araneidae, and divided Araneidae into the three subfamilies (Araneinae, Metinae and Tetragnathinae). He included several genera, such as *Meta*, *Metellina*, *Metleucauge*, and *Leucauge*, in Metinae. He stated that *Meta* and the related genera have many primitive morphological characters, and that the genera resemble some genera of Theridiidae, a family of

Araneoidea. Recently, Levi (1986) divided Araneidae again into two families, Araneidae and Tetragnathidae, with the latter including Metinae and Tetragnathidae described in the previous paper.

I report here on the predatory behavior of the three Japanese species of *Metleucauge* (*M. kompirensis*, *M. yunohamensis*, and *Metleucauge* sp.). These species do not use immobilization wrapping at all. I also discuss the evolution of the predatory behavior in the Tetragnathidae-Metinae line.

Metleucauge sp. has been thought to be *Meta segmentata* previously by Japanese arachnologists. But Shinkai and Takano (1984) stated that it belongs to *Metleucauge*, and that they regarded it as *Metleucauge segmentata*. Recently, Yaginuma (1986) said that its species name is not *segmentata*, though it belongs to *Metleucauge*. He said that it resembles *M. yunohamensis*, but is a new species of *Metleucauge*.

MATERIALS AND METHODS

The investigation of *M. kompirensis* and *M. yunohamensis* was done in 1986 and 1987 at two mountain streams in Kyoto city (100-200 m above sea level). *M. yunohamensis* matured in April to May, and *M. kompirensis* matured in June to July. The species usually made their horizontal orb-webs above the mountain streams. I observed the predatory behavior of adults of the two species, both with natural prey and with the fairly large prey given by me. The latter prey were collected using a sweep-net near the study area. Less than two prey were attached to a web by a pincette. I observed predatory behavior of many individuals of *M. kompirensis* for several hundred hours, and of *M. yunohamensis* for several tens of hours. The body length of both the spiders and the prey was estimated by eye.

The third species, *Metleucauge* sp., was investigated halfway up Mt. Chougatake, north of Nagano Prefecture (ca 1400 m above sea level). This species, like *kompirensis* and *yunohamensis*, also usually made its web above mountain streams. I could observe the predatory behavior for only ten to several hours.

RESULTS

Predatory behaviors.—The following behaviors were observed in the context of predatory sequences:

Jerking: This consists of a rapid pulling of the radii with the first pair of legs.

Web-Shaking: Only *M. yunohamensis* showed this behavior. This species sometimes shook the web slowly with legs I (and II?) as soon as the prey hit the web. This is different from jerking, because the web was pulled perpendicularly to its plane. The function of the low frequency vibration is unknown.

Approach to prey: Running or walking from the hub to the capture site along the radial thread(s), pulling a drag-line from the hub. Running occurred generally when the prey was vibrating rapidly, while walking occurred generally when the prey was motionless (not vibrating).

Touch: The spiders touch the prey with legs I (and palps?) before most attacks are initiated. *Metleucauge* species often touched the prey with legs I in unsuccessful prey capture sequences, whereas touching was not observed at all in

successful prey capture sequences. Touching might have occurred also in the latter case, but may have occurred too rapidly to detect without high-speed film.

Seizing in jaws: Seizing and holding the prey in the chelicerae.

Biting: Biting the prey with the chelicerae. Lubin (1980) included both seizing and biting in biting. Certainly the jaws are used both in seizing and biting, but there are some differences between them. Robinson and Robinson (1973) pointed out that seizing is used mainly with very small prey, whereas biting is used mainly with larger prey, and that the time required for seizing was very short, whereas the time required for biting was several times longer than that for seizing. So, I intend to distinguish seizing from biting.

Wrapping: Wrapping was used only after prey immobilization in *Metleucauge* species. Wrapping occurred at three sites: at the capture site, during transportation to the hub, and at the hub itself. At the capture site, wrapping generally began after immobilization biting while the prey was still in the spider's jaws. I called this type of wrapping, also observed in *Tetragnatha praedonia*, as "wrapping with bite" (Yoshida 1987). After "wrapping with bite", *Metleucauge* released the prey from its jaws, and then cast additional skeins of silk onto the prey. Wrapping was often interrupted by cutting the prey from the web. Free-wrapping (wrapping the prey beneath the web) was rarely observed. *Metleucauge* was different from *Argiope argentata*, because it never rotated the prey around a radius while wrapping ("roisserie" wrapping of Eberhard [1982]).

Pulling out: Pulling the prey from the web, using the jaws.

Cutting out: Cutting the web in order to remove the prey from the web.

Carrying in jaws: Carrying the prey in the jaws to a feeding site.

Carrying on silk: Carrying the prey to the feeding site, suspended on a silk line from the spinnerets. The silk line made by *M. yunohamensis* was short, so the prey sometimes became entangled in the web. In these circumstances, the web was destroyed, as the spider pulled the prey out by force. Other species did not show this behavior.

Leaving the prey: The return of the spider to the hub alone, leaving the prey at the capture site.

Predatory sequences employed.—Three predatory sequences were observed in *M. kompirensis* and *M. yunohamensis* as follows:

Seize-Pull out: Spiders generally located prey by jerking the web, then ran to the prey, seized it in the jaws and pulled it from the web. Spiders then carried the prey in the jaws to the hub. In most cases, spiders returned by dropping from the web, hanging with the dragline attached to the hub, and then climbed quickly to the hub along the dragline ("drop and climb up" behavior). It took only 2-5 seconds for the spiders to complete seize-pull out sequences.

Bite-Pull out: This sequence resembles seize-pull out, the above sequence, but it includes the behavior unit "biting". The time to seize the prey was very short (perhaps less than one second), but biting took several seconds to several minutes. Probably spiders would infuse the venomous fluid into the prey during biting. Spiders usually bit some parts of a large prey first for a fairly long time (more than several seconds), and then they changed the biting sites successively. As a result, the prey was crushed gradually into a ball. Then the spider pulled it from the viscid spirals with the jaws. The prey were carried either by drop and climb-up mentioned above, or carrying the prey along a radial thread.

Bite-Wrap: The prey were immobilized by biting. After immobilization biting, spiders first wrapped the prey with silk while it was still in the jaws. Then they

Table 1.—Attack sequences with different types of prey in three species of *Metleucauge*. Frequency of occurrence of the different sequences is shown after each sequence.

Prey type	<i>M. kompirensis</i>		<i>M. yunohamensis</i>		<i>Metleucauge</i> sp.	
Diptera	Seize-Pull Out	54	Seize-Pull Out	4	Seize-Pull Out	0
	Bite-Pull Out	2	Bite-Pull Out	1	Bite-Pull Out	1
	Bite-Wrap	0	Bite-Wrap	11	Bite-Wrap	3
Ephemeroptera	Seize-Pull Out	18	Seize-Pull Out	0	Seize-Pull Out	0
	Bite-Pull Out	0	Bite-Pull Out	0	Bite-Pull Out	0
	Bite-Wrap	0	Bite-Wrap	5	Bite-Wrap	2
Lepidoptera	Seize-Pull Out	0	Seize-Pull Out	0	Seize-Pull Out	0
	Bite-Pull Out	1	Bite-Pull Out	0	Bite-Pull Out	0
	Bite-Wrap	12	Bite-Wrap	4	Bite-Wrap	1
Hymenoptera	Seize-Pull Out	1				
	Bite-Pull Out	0				
	Bite-Wrap	0				
Plecoptera	Seize-Pull Out	0			Seize-Pull Out	0
	Bite-Pull Out	0			Bite-Pull Out	0
	Bite-Wrap	1			Bite-Wrap	1
Odonata	Seize-Pull Out	0				
	Bite-Pull Out	4				
	Bite-Wrap	12				
Orthoptera	Seize-Pull Out	0				
	Bite-Pull Out	1				
	Bite-Wrap	0				
Neuroptera					Seize-Pull Out	0
					Bite-Pull Out	1
					Bite-Wrap	0

wrapped further after releasing it from the jaws. When the prey was large, wrapping was often interrupted by cutting the silk entangling the prey. The silk covered only some parts of the prey, perhaps because the amount of silk was little. Finally, spiders cut out all the entangling silk lines, in order to remove the prey from the web. In most cases, the prey were carried to the hub suspended on a silk line. *Metleucauge* sp. used bite-pull out and bite-wrap, but did not use seize-pull out.

Frequency of sequences with different types of prey and efficiency of predation on various types of prey.—Table 1 shows the comparison of attack sequences with different types of prey in three species of *Metleucauge*. The wrap-bite sequence, frequently used by *Argiope*, was not used by the spiders at all. With Diptera and Ephemeroptera, *M. kompirensis* used mainly seize-pull out and did not use bite-wrap at all, while *Metleucauge* sp. used mainly bite-wrap with Diptera and Ephemeroptera, and did not use seize-pull out at all. *M. yunohamensis* used only bite-wrap with Ephemeroptera, and used mainly bite-wrap with Diptera. Lepidoptera and Odonata were attacked mainly by bite-wrap.

Table 2 shows the efficiency of predation (% of prey insects captured to the total insects attached to the webs) on various types of prey in each species. Diptera, Ephemeroptera, and Lepidoptera were captured efficiently by all species, though few data are available for *Metleucauge* sp. Damselflies were captured efficiently also by *M. kompirensis*. Hemiptera (stink bugs and leafhoppers) was not captured at all. And Orthoptera and Hymenoptera was captured only once,

Table 2.—Efficiency of predation on various types of prey. Numerals show the number of prey captured or not captured by each spider species. Numerals in parentheses show the percentages.

Prey type	<i>M. kompirensis</i>		<i>M. yunohamensis</i>		<i>Metleucauge</i> sp.	
	Captured	Not Captured	Captured	Not Captured	Captured	Not Captured
Diptera	56 (91.6)	2 (8.4)	16 (100)	0 (0)	4 (66.7)	2 (33.3)
Ephemeroptera	18 (100)	0 (0)	5 (100)	0 (0)	2 (100)	0 (0)
Lepidoptera	12 (80.0)	3 (20.0)	4 (80.0)	1 (20.0)	1 (100)	0 (0)
Odonata	16 (72.7)	6 (23.3)	—	—	—	—
Hymenoptera	1 (50.0)	1 (50.0)	0 (0)	5 (100)	0 (0)	2 (100)
Hemiptera	0 (0)	5 (100)	0 (0)	3 (100)	—	—
Orthoptera	1 (10.0)	9 (90.0)	—	—	—	—
Coleoptera	—	—	0 (0)	3 (100)	—	—
Plecoptera	1 (100)	0 (0)	—	—	1 (100)	0 (0)
Neuroptera	—	—	—	—	1 (50.0)	1 (50.0)
Mecoptera	—	—	—	—	0 (0)	1 (100)
Dermaptera	—	—	—	—	0 (0)	1 (100)
Lepidoptera (larva)	—	—	—	—	0 (0)	2 (100)
Total	105 (80.1)	26 (19.9)	25 (67.6)	12 (32.4)	9 (50.0)	9 (50.0)

respectively. When failing in prey-capture, the spider often touched the prey with leg(s) I.

The spiders failed to capture Hemiptera, Orthoptera, Hymenoptera and Coleoptera 28 times (93% of these insects given), and there were several types of failures: 1) spiders did not respond to the prey (four times), 2) the spider only jerked its web (once), 3) prey escaped before the spiders arrived at the capture sites (three times), 4) the spider approached its prey, but then returned to the hub, leaving the prey at the capture site (once), 5) spiders tried to bite the prey, but returned to the hub without biting (it is unknown why they did not bite: five times). Of these, one spider touched the prey before attempting to bite, and two spiders dropped the prey from the webs after attempting to bite, 6) spiders returned to the hub after prey-touching (nine times), 7) spiders dropped their prey after prey-touching (four times), 8) the spider bit its prey, but dropped it after prey-touching (once).

Prey-touching was observed with 54% (15/28) of the insects not captured, very often with Hemiptera (7/8), but was not observed at all with Coleoptera (0/3). This behavior occurred mainly before returning to the hub alone and prey-dropping (13/15). This prey-touching behavior was not observed at all when the spider succeeded in capturing the prey.

Figs. 1-3 show the relation between the relative body length (prey/spider) and the predatory sequences employed in each species. Seize-pull out was used with very small prey (smaller than half a spider body length or so), while bite-wrap was used mainly with larger prey. Bite-pull out, whose frequency was low, was used with prey of intermediate size.

Figs. 1-3 also show the relative body length of prey insects not captured by spiders. It ranged widely. In some cases, such as Diptera, Lepidoptera, Hymenoptera, Orthoptera (the prey of *M. kompirensis*), Neuroptera (the prey of *Metleucauge* sp.), the insects that escaped were larger than ones captured, suggesting that larger prey cannot be captured easily. However, the prey insects that escaped from webs of *Metleucauge* sp. were smaller than ones captured. In

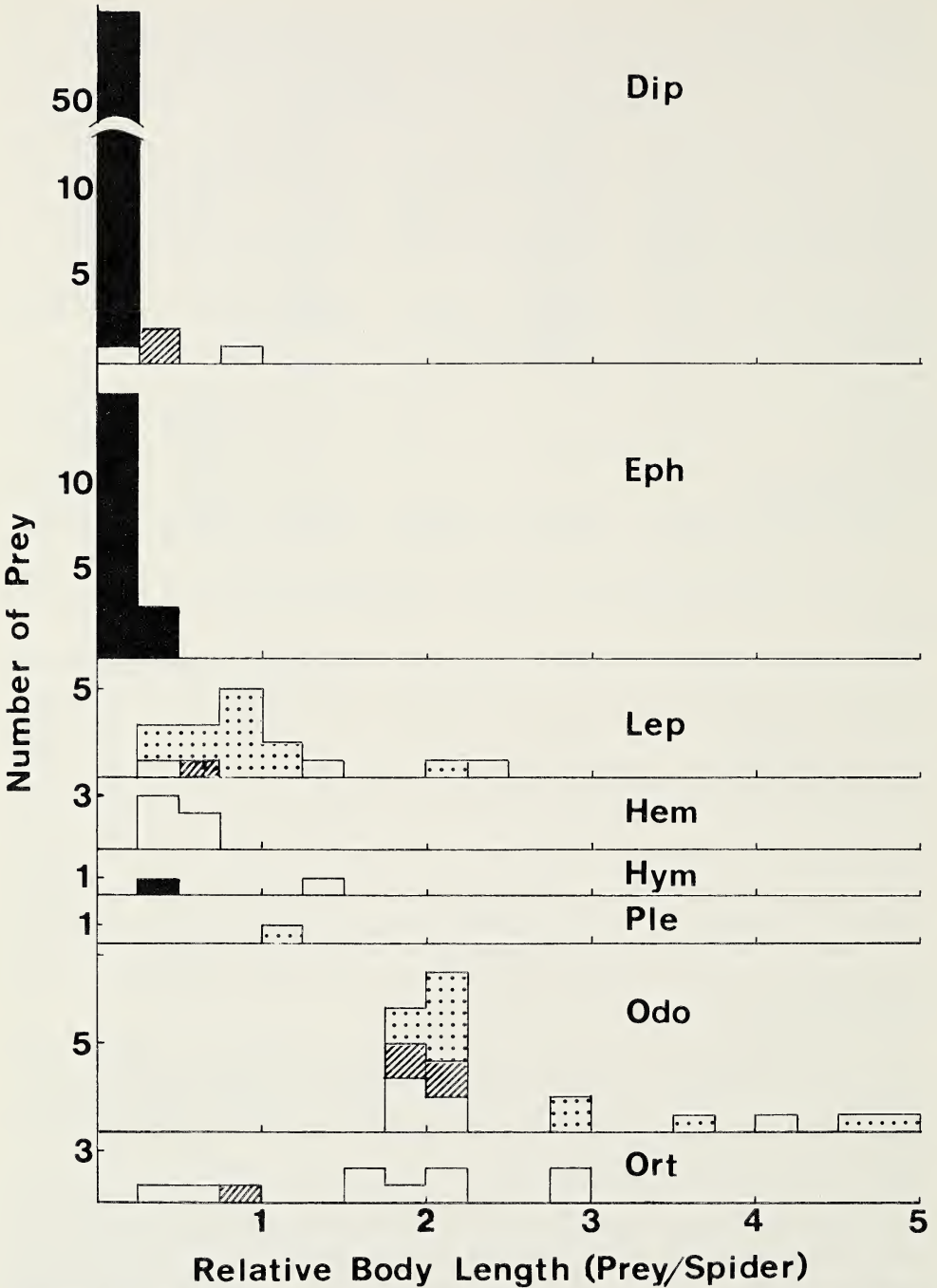


Figure 1.—The relation between predatory sequences of *Metleucauge kempirensis* used to immobilize prey and the relative body length (prey/spider) of various kinds of prey. Dip = Diptera, Eph = Ephemeroptera, Lep = Lepidoptera, Hem = Hemiptera, Hym = Hymenoptera, Ple = Plecoptera, Odo = Odonata, Ort = Orthoptera. Each area shows the cases in which prey insects were captured by the following sequence. Solid = seize-pull out, Shaded: = bite-pull out, Dotted = bite-wrap sequence. Open area shows the case in which prey insects were not captured by spiders.

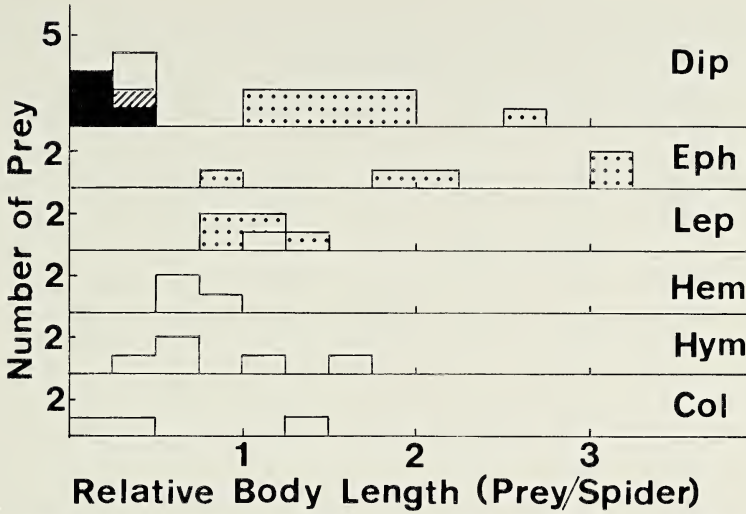


Figure 2.—The relation between predatory sequences of *Metleucauge yunohamensis* used to immobilize prey and the relative body length (prey/spider) of various kinds of prey. Dip = Diptera, Eph = Ephemeroptera, Lep = Lepidoptera, Hem = Hemiptera, Hym = Hymenoptera, Col = Coleoptera. Each area shows the cases in which prey insects were captured by the following sequence. Solid = seize-pull out, Shaded = bite-pull out, Dotted = bite-wrap sequence. Open area shows the case in which prey insects were not captured by spiders.

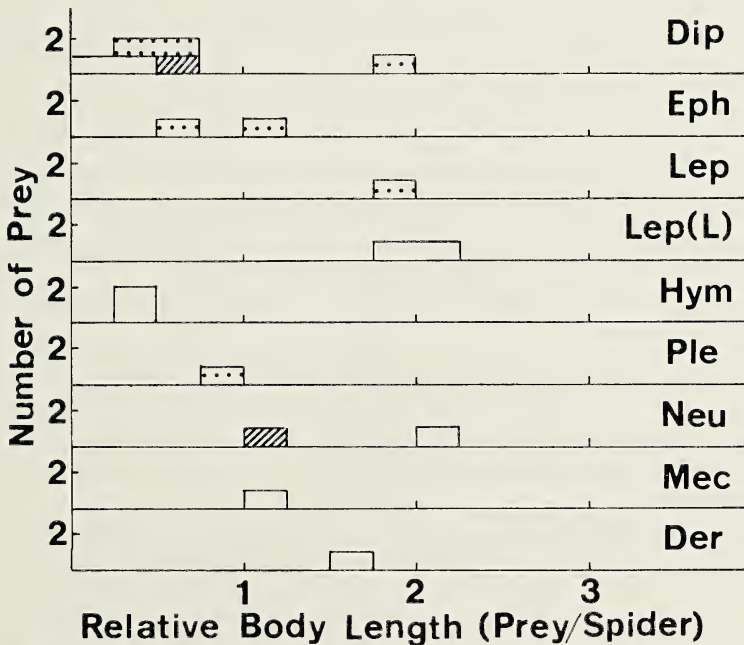


Figure 3.—The relation between predatory sequences of *Metleucauge* sp. used to immobilize prey and the relative body length (prey/spider) of various kinds of prey. Dip = Diptera, Eph = Ephemeroptera, Lep = Lepidoptera, Lep(L) = Lepidoptera (larva), Hym = Hymenoptera, Ple = Plecoptera, Neu = Neuroptera, Mec = Mecoptera, Der = Dermaptera. Each area shows the cases in which prey insects were captured by the following sequence. Solid = seize-pull out, Shaded = bite-pull out, Dotted = bite-wrap sequence. Open area shows the case in which prey insects were not captured by spiders.

Table 3.—Prey collected in the webs of *Metleucauge kompsonensis*.

Prey	Body length in mm							Total (%)
	0–2.0	–4.0	–6.0	–8.0	–10.0	–12.0	>12.0	
Diptera								
Nematocera	4023	559	24	5	0	1	0	4612(91.7)
Brachycera	7	3	1	0	0	0	0	11(0.2)
Hemiptera	85	25	0	0	0	0	0	110(2.2)
Ephemeroptera	6	103	134	22	4	2	3	274(5.4)
Plecoptera	0	3	0	3	0	0	0	6(0.1)
Hymenoptera	7	1	0	0	0	0	0	8(0.2)
Psocoptera	1	0	0	0	0	0	0	1(0.0)
Trichoptera	0	0	1	0	0	0	0	1(0.0)
Collembola	5	0	0	0	0	0	0	5(0.1)
Acarina	1	0	0	0	0	0	0	1(0.0)
Araneae	1	0	0	0	0	0	0	1(0.0)
Total	4136	694	160	30	4	3	3	5030
(%)	(82.2)	(13.8)	(3.2)	(0.5)	(0.1)	(0.1)	(0.1)	

the case of Odonata given to *M. kompsonensis* and Lepidoptera to *M. yunohamensis*, there was no clear trend in relation to size. Likewise, the low capture efficiency of Hemiptera, Orthoptera, Hymenoptera, and Coleoptera, was not always dependent on prey size. For example, Hemiptera were not captured at all in spite of their small size.

The prey collected in the webs of *M. kompsonensis* and *M. yunohamensis*.—Table 3 shows the prey collected from April to July in the webs of *M. kompsonensis*. Of 5030 prey, dipteran insects totalled 4623 (91.9%). Almost all Diptera belonged to Nematocera. Thus, nematoceros flies are the main prey of the spider. Aside from Diptera, Ephemeroptera (mayflies) and Hemiptera (winged aphids) were relatively abundant. Other prey occurred rarely, such as Plecoptera, Hymenoptera and Collembola. These prey were generally small (96% of them were smaller than 4 mm in body length), though Ephemeroptera were relatively larger than the other prey. Potentially dangerous insects, such as wasps and pentatomids, were not collected at all, though tiny braconids were collected in small numbers.

Table 4 shows the prey collected in May in the webs of *M. yunohamensis*. Though the number of prey collected was smaller, it shows a similar trend as *M. kompsonensis* (Table 1). That is, the main prey items were nematoceros flies; Ephemeroptera was the next abundant prey; the prey were generally small except for Ephemeroptera.

I could not collect the prey in the webs of *Metleucauge* sp. because the density of the webs was very low and I had not enough time to collect the prey.

DISCUSSION

Levi (1980) regarded *Meta* and the related genera as primitive in Araneidae, judging from several morphological and behavioral characters, such as eye placement, eye structure, male palpi, female genitalia and mating behavior.

This study showed that *Metleucauge* used three predatory sequences (seize-pull out, bite-pull out, and bite-wrap). Which sequence is used is generally dependent

Table 4.—Prey collected in the webs of *Metleucauge yunohamensis*.

Prey	Body Length in mm							Total (%)
	0-2.5	-5.0	-7.5	-10.0	-12.5	-15.0	>15.0	
Diptera								
Nematocera	529	28	0	0	0	1	0	558(84.7)
Brachycera	2	0	0	0	0	0	0	2(0.3)
Hemiptera	2	0	0	0	0	0	0	2(0.3)
Ephemeroptera	1	21	56	10	4	1	3	96(14.6)
Lepidoptera	1	0	0	0	0	0	0	1(0.2)
Total	535	49	56	10	4	2	3	659
(%)	(81.2)	(7.4)	(8.5)	(1.5)	(0.6)	(0.3)	(0.5)	

on prey size, that is, seize-pull out is used for small prey, on the contrary, bite-wrap for larger prey. Body weight, not body length, of the prey will have to be measured in order to ascertain the accurate limits for which a different sequence is used. The spiders may decide whether the prey should be captured or not by touching it with legs I. The lack of attack wrapping is another remarkable characteristic of the predatory behavior of *Metleucauge*.

Although the predatory behavior in Metinae has not been studied in detail, Eberhard (1982) found that *Leucauge* spp. and *Chrysometa* spp. used attack (=immobilization) wrapping. *Leucauge magnifica* also often uses attack wrapping (Yoshida, unpub. data). The lack of attack wrapping of three Japanese species of *Metleucauge* therefore may suggest that Metinae represent the primitive evolutionary stages of predatory behavior (Robinson et al. 1969). This behavioral primitiveness is consistent with the primitiveness of other morphological and behavioral characters (Levi 1980). The lack of attack wrapping can be also explained in another manner, that is, the habit may have been lost secondarily (Levi 1985).

Robinson (1975) listed two merits of attack wrapping: one is the economy of the time absent from the hub, and another is the ability to attack large and/or potentially dangerous prey without the dangers involved in the intimate contact of a biting attack. Furthermore, he said that attack wrapping is never lost because its merits were too large. By which manner can the lack of attack wrapping in *Metleucauge* be explained?

The three Japanese species of *Metleucauge* usually make their webs above mountain streams, as shown earlier, and the fourth species, *M. eldorado*, also "makes an orb—between rocks near streams" (Levi 1980). Many insects (mayflies, midges, stoneflies, caddisflies, damselflies, dragonflies) fly above streams. As shown in the results, the main prey of *M. kompirensis* and *M. yunohamensis* are mayflies and midges. Eberhard (personal communication) pointed out that the prey left in the webs may not be the main prey if they are not attacked by the spiders. However, *M. kompirensis* actually feeds mainly on midges and mayflies based on my many observations. These insects are weak fliers, and can be immobilized easily by biting without danger. *Metleucauge* species seem to be accustomed to handling these insects, since the spiders ran to the prey rapidly and without hesitating when mayflies or midges were caught in their webs. Other insects flying above streams are rarely captured by the webs. For example, there are many agriid damselflies in the habitat of *M. kompirensis*, but I saw them captured only a few times during several years of investigation.

When presented with an unusual prey, not normally trapped under natural conditions (such as pentatomids or grasshoppers), the spiders approached slowly and hesitantly to the prey, often touching the prey with legs I. This suggests that *Metleucauge* species are not accustomed to such types of prey.

Another merit of attack wrapping, economy of time away from the hub, seems to be a lesser difficulty for these species. Because mayflies and midges are frequently captured, and are firmly restrained by the webs, the spiders need not handle the prey in a hurry in order to capture the next prey. Given these conditions, the ability to attack wrap may have been lost. This discussion suggests that if the ancestor of *Metleucauge* had the ability to attack wrap, and if potentially dangerous prey were included in the prey, the ability may have not been lost. In this respect, it is important to ascertain whether the species of *Meta* and *Metellina* can attack wrap prey, and also, what kinds of prey they eat in nature. During 1987 I conducted a preliminary investigation of the predatory behavior of *Meta reticuloides* and found that some spiders attempted to immobilize an ant by wrapping. It appears that species related to *Metleucauge* may have the ability to attack wrap and that this may result from a difference in prey items. The predatory behavior of *Meta* and *Metellina* must be studied and be compared with that of *Metleucauge*.

If attack wrapping was fully developed (as seen, for example, in *Argiope*) in the ancestor of *Metleucauge*, this ability may not have been lost. But, if the ability was incomplete in its development, as occurs in *Leucauge magnifica* (Yoshida, unpub. data), and if incomplete ability does not have much advantage, it may have been easily lost. Other spiders such as *Mastophora* and *Dichrostichus* may also have lost attack wrapping because all the prey are non-dangerous moths and must be captured rapidly (Eberhard, pers. comm.).

I can not decide now whether the lack of attack wrapping is a primitive character or has been lost secondarily. Thorough study of the predatory behavior of genera related to *Metleucauge* (*Meta*, *Metellina*, *Chrysometa* and *Homalometa*) may solve this question.

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SPIDERS OF WASHINGTON COUNTY, MISSISSIPPI

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ABSTRACT

Over a seven-year period, approximately 35,000 spiders representing 26 families, 133 genera, and 234 species were captured in Washington County, Mississippi, by pitfall, sweepnet, vacuum, bag, and hand. Specimens were collected in 10 different habitat types and in four vegetational strata. Old-field habitats yielded the most species (152) and residential lawns the fewest (14). Considering all habitats sampled, the ground layer produced 111 species, the herbaceous strata 133, the shrub layer 49, and the tree strata 30 species. The sweepnet method of capture obtained 128 species, pitfall 95, hand 61, vacuum 53, and bagging 19 species. The largest number of species were obtained in spring and early summer (maximum of 125 in May), with the fewest in mid-winter (Jan. = 24). Twenty-one species were considered abundant, 51 common, 67 uncommon, and 95 rare. Additions to the state list of Dorris (1972) number 102 species, for a new state total of 364 species.

A comparison with the North American fauna and with other surveys indicates that Washington County is underrepresented both in cursorial forms active on the soil surface and web-spinning forms typical of undisturbed habitats. The high incidence of disturbed habitats associated with intensive agricultural activities in Washington County seems to have produced a depauperate spider fauna, but spider populations of certain species characteristic of disturbed habitats are of sufficiently high density and broad distribution to have a potential affect on crop insect pests.

INTRODUCTION

Stoneville, Mississippi is the site of the Delta Branch Experiment Station, Mississippi State University, and the Delta States Research Center, U.S. Department of Agriculture. For more than 50 years, scientists have been

observing, collecting, and experimenting with the arthropods associated with crops on site and in the surrounding Washington County. In the last 25 years, much of that effort has been directed toward the arthropods of cotton and adjacent habitats (e.g., Pfrimmer 1964; Stadelbacher 1981). Although spiders have been indicated as potentially important predators in cotton, they have usually not been identified to the genus or species level (e.g., Pfrimmer 1964; Smith and Stadelbacher 1978). Over the last 10 years, the improved status of spider taxonomy and a broad awareness of spiders as biological control agents has changed the research environment concerning field studies of spiders in agricultural situations (Riechert and Lockley 1984).

Beginning in 1981, field collections have attempted to delineate the structure and composition of spider populations in the Stoneville environs. Since 1984, we have focused on the spiders in habitats adjacent to cotton, particularly those species that could be determined to be predators of the tarnished plant bug, *Lygus lineolaris* (Palisot) (Heteroptera: Miridae). These have included *Oxyopes salticus* Hentz (Oxyopidae), *Phidippus audax* (Hentz) (Salticidae), and *Pisaurina mira* (Walckenaer) (Pisauridae) (Lockley and Young 1986a, b; Lockley et al. 1989; Welbourn and Young 1988; Young 1989a, b, c, d; Young and Lockley 1985, 1986, 1988, 1989a, b). The purpose of this report is to present the results of seven years of sampling for spiders in Washington County. These data are compared with other studies, and the potential role of this assemblage of spiders as agents for crop pest suppression is discussed.

METHODS AND MATERIALS

Washington County, Mississippi, is in the west-central portion of the state, adjacent to the Mississippi River, and in the approximate center of the Yazoo-Mississippi Delta. This delta began formation about 18,000 years ago at the end of the last ice age and is ideally suited for intensive agriculture (Fisk 1944). Deep alluvial deposits, a flat terrain, ample moisture, hot and humid summers, and mild winters combine to facilitate the growth of plants, and their associated arthropods. Washington County contains ca 200,000 ha, of which ca 122,000 ha (61%) are under cultivation in such crops as cotton, rice, milo, and soybean. Timbered areas comprise ca 44,000 ha (22%) and include several state and federal parks and wildlife refuges in addition to areas located outside the levees. There are 1,365 km of roads in the county which, assuming an average width of 12 m, occupy 18,000 ha (9%). The remaining 16,000 ha (8%) are composed of residential and business areas, lakes, waterways, standing water, and marshes (Gunn et al. 1980). This pattern of land use provides a high percentage of "disturbed" habitats. All crop fields are routinely plowed, cultivated, sprayed with herbicides and insecticides, and otherwise made inhospitable for arthropods. "Edge" habitats—edge of road, edge of ditch, edge of crop field, edge of forest island, edge of wet area, etc.—also are typically disturbed areas that are mowed, sprayed with herbicides, cultivated, or otherwise intruded upon at irregular intervals. These disturbed habitats, combined with residential and business lawns and gardens, probably comprise over 75% of the county area.

Beginning in 1981, systematic sampling of a variety of habitats, both disturbed and undisturbed, was conducted utilizing five collection methods (Table 1).

Table 1.—Sampling effort for spiders in Washington County, Mississippi, 1981-1987.

Habitat or host plant	Sampling period	Freq. of collect.	Method of coll.	No. of samples	No. of spiders
Soybeans	VII-IX-81	Weekly	Sweep	40	1816
Forest	VI-82-VI-83	Biweekly	Pit	25	227
<i>Erigeron</i> spp.	IV-IX-84	We	Swp	136	909
Forest	IV-VI-84	We	Pit	45	278
Old-field	V-XII-84	We	Vac	103	332
Pasture	VI-VIII-84	We	Vac	9	1800
<i>Erigeron</i> spp.	IV-IX-85	We	Swp	104	782
Cotton margins	II-XII-85	Bi	Vac	140	1867
Old-field	III-85-V-86	Bi	Pit	117	1674
Margins, pasture, old-field	X-85-X-86	Bi	Swp, Vac	487	8994
<i>Erigeron</i> spp.	III-IX-86	We	Swp	502	3471
Roadside grass	IV-VI-86	We	Vac	336	7459
Margin flowers	V-86-IV-87	Monthly	Swp	34	317
Spanish Moss	V-86-V-87	Mo	Bag	15	613
Forest margins	IX-XI-86	We	Swp	54	1393
Misc. habitats	1981-87	—	Hand	—	3109
Totals				2147	35041

Ground-dwelling spiders were sampled with several types of pitfall traps, some with covers and some with interception barriers. Vegetation above the soil surface was sampled with a dense muslin-mesh sweepnet, diameter 39 cm. A motorized suction device (D-vac®) with a 34 cm diameter opening and a nozzle speed of ca 100 km/h was used to sample all strata, as was the technique of capturing specimens by hand. Terminal portions of tree branches containing Spanish moss also were bagged and removed. Over the seven-year period, samples were obtained during every week of the year and every hour of the diel. Samples were brought into the laboratory and frozen at -20°C until they could be examined and then thawed, sorted, identified, counted, and recorded. Voucher specimens and unidentified material were stored in alcohol for later processing.

Representatives of every spider species were examined by G. B. Edwards, A. R. Brady, Hope College, Holland, Michigan, or D. B. Richman, New Mexico State University, Las Cruces, New Mexico. Voucher specimens are deposited at the Mississippi Entomological Museum, Miss. State University, Starkville, in the personal collection of T. C. Lockley, and in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville.

RESULTS AND DISCUSSION

Within-county comparisons.—At least 234 species of spiders in 133 genera and 26 families were identified from ca 35,000 specimens collected over a seven-year period (Appendix 1). This assemblage occurred primarily (203 spp.) in ecotonal areas such as the margins of roads, fields, forests, and water, and in early-successional habitats such as old-fields and pastures (Table 2). Old-field habitats, 2-5 years post-cultivation and abandonment, contained the highest diversity of spiders (152 spp.), but represented one of the rarest habitat-types in a county under intense agricultural management. Road and crop-field margins contained the second-highest diversity of spiders—98 spp.—and represented considerably

Table 2.—Number of spider species distributed among various parameters, Washington County, Mississippi.

Strata	Method of capture	Abundance
Ground.....111	Pitfall..... 95	Rare..... 95
Herb.....133	Sweep.....128	Uncommon.....67
Shrub..... 49	Vacuum..... 53	Uncommon.....51
Tree..... 30	Hand..... 61	Abundant.....21
	Bag..... 19	
Habitat		
Forest..... 33	Lawn, resid..... 14	
Transitional (T)..... 49	Building..... 17	
Crop, Field..... 43	Spanish moss..... 17	
Meadow, Grassland (M)..... 23		
Old-field (O).....152	Combine, M,R.....101	
Water margin (W)..... 16	Combine, T,O,W.....169	
Road, Field margin (R)..... 98	Combine, M,R,T,O,W.....203	

more acreage than old-fields. Cotton and soybean fields, though representing over 50% of the county surface area, contained only 43 species. Thus only 19% of the spider species available in the county for predation on crop pests actually occurred on crops. Fortunately for crop pest control, most local pests (e.g., *Anthonomus* spp., *Heliothis* spp., *Lygus* spp.) also occupy habitats adjacent to crops at some time in their life cycle. Because no spider species was found exclusively on crops, potentially as many as 234 species may prey on crop pests in these adjacent habitats.

The diversity of spiders obtained by our collection methods was low in the winter months, with a minimum of 24 species collected in January (Fig. 1). Spider populations dramatically increased in April, and by May 125 species were active. The number of species captured each month gradually declined through the summer and fall, with 62 species still active in October. Twenty-one species were considered "abundant" in the habitats in which they occurred (Table 2). These included 11 species that were abundant in cotton, as well as in adjacent habitats. Given the large amount of acreage devoted to cotton, these 11 species were probably the most abundant spiders in Washington County and may have a major impact on cotton insect pests. They were *Neoscona arabesca* (Walck.), *Tetragnatha laboriosa* Hentz, *Ceraticelus emertoni* (O. P.-Camb.), *Lycosa lenta* group, *Lycosa rabida* Walck., *Pardosa milvina* (Hentz), *Oxyopes salticus* Hentz, *Pisaurina mira* (Walck.), *Metaphidippus galathea* (Walck.), *Phidippus audax* (Hentz), and *P. clarus* Keys. Several of these species are important predators in Washington County on the tarnished plant bug, *Lygus lineolaris* (Young 1989a, b, c, d). They may also have an affect on the cotton bollworms, *Heliothis* spp. (Stadelbacher and Lockley 1983), and the sterile bollworm hybrids and braconid parasites currently under consideration as control agents of the bollworms. The most abundant spider species in forested areas were *Agelenopsis naevia* (Walck.) and *Gladicosa gulosa* (Walck.); in Spanish moss, *Methaphidippus tillandsiae* Kaston; in roadside and field margins, *Oxyopes salticus* and *Ceraticelus emertoni*; in old-fields, *Pardosa milvina*, *Schizocosa* spp., *Xysticus ferox* (Hentz), and *Tetragnatha laboriosa*; and on *Erigeron* spp. (Compositae), *Metaphidippus galathea* and *Misumenops asperatus* (Hentz).

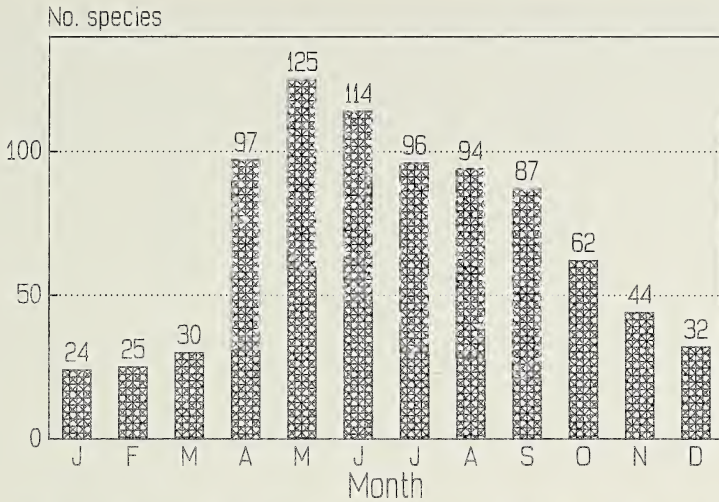


Figure 1.—Maximum number of spider species captured each month during 1981-1987 in Washington Co., Mississippi.

The sweepnet method of spider capture obtained 55% (128 spp.) of the fauna in Washington County (Table 2), and was the most frequently used capture technique. The vacuum method obtained the least number of species (53), but did produce five species not captured by other means. This collection technique probably could have been eliminated, with the resultant savings in time and effort more profitably directed toward other methods of collection.

The highly disturbed nature of most of the soil in Washington County suggests that typical soil spiders should be under-represented. Ground-dwelling spiders, obtained primarily by pitfall traps, represented 47% (111 spp.) of all species (Table 2), whereas foliage-dwelling spiders represented 70% of the species total (some species occupied both ground and foliage strata). For comparison, a three-year study conducted in frequently-disturbed soybean fields in Delaware indicated that 70% of the species occurred on foliage and only 32% occurred on the ground (Culin and Rust 1980). Conversely, a study that included sampling of deep leaf-litter in undisturbed Kansas woodland indicated that 75% of the species were ground-dwelling and 25% foliage-dwelling (Fitch 1963). Most of the forested area in Washington County is covered with water at some time each year, due either to flooding of the Mississippi River or to slow run-off after heavy rains. Leaf-litter depth is typically shallow or non-existent in these areas and, combined with the inundation, probably supports a very depauperate spider fauna (e.g., Uetz et al. 1979). Thus it is not surprising that, considering all habitats sampled, foliage-dwelling spiders are relatively very well-represented in Washington County.

Comparison with the North American fauna.—In 1985, V. D. Roth published a compilation of the families and genera of spiders known to occur in North America. He also included an estimate of the number of species in each genus. This information now permits a comparison of limited-area surveys with the entire North American fauna. In Washington County, specimens were obtained from 26 families and 133 genera (Table 3). This represents 54% of the 48 families and 28% of the 469 genera (Roth 1985) occurring in North America. The 234 species from Washington County represent only 7% of the 3311 North American

Table 3.—Proportion of genera and species of the North American spider fauna (Araneomorphae) that occur in Washington County, Mississippi.

Family	Genera			Species		
	N.A.	Wash. Co.	%	N.A.	Wash. Co.	%
Agelenidae	25	2	8	252	3	1
Amaurobiidae	8	—	—	82	—	—
Anapidae	1	—	—	1	—	—
Anyphaenidae	5	4	80	37	6	16
Aphantochilidae	1	—	—	1	—	—
Araneidae	42	23	55	192	39	20
Caponiidae	2	—	—	3	—	—
Clubionidae	20	8	32	193	13	7
Ctenidae	3	—	—	5	—	—
Desidae	1	—	—	1	—	—
Dictynidae	9	1	11	159	2	1
Diguetidae	1	—	—	6	—	—
Dinopidae	1	—	—	1	—	—
Dysderidae	3	1	33	7	1	14
Filistatidae	3	1	33	13	1	8
Gnaphosidae	24	12	50	248	25	10
Hahniidae	3	2	67	19	3	16
Hersiliidae	1	—	—	2	—	—
Homalonychidae	1	—	—	2	—	—
Hypochilidae	1	—	—	4	—	—
Leptonetidae	2	—	—	34	—	—
Linyphiidae	152	11	7	845	17	2
Loxoscelidae	1	1	100	13	2	15
Lycosidae	15	10	67	234	32	14
Mimetidae	2	1	50	13	1	8
Mysmenidae	3	—	—	6	—	—
Nesticidae	3	1	33	31	1	3
Ochyroceratidae	1	—	—	1	—	—
Oecobiidae	2	1	50	7	1	14
Oonopidae	8	1	13	24	1	4
Oxyopidae	3	2	67	20	2	10
Philodromidae	5	3	60	95	7	8
Pholcidae	10	3	30	31	3	10
Pisauridae	4	3	75	14	4	29
Plectreuridae	2	—	—	15	—	—
Salticidae	45	25	55	288	47	16
Scytodidae	1	1	100	9	1	11
Selenopidae	1	—	—	5	—	—
Sparassidae	3	—	—	8	—	—
Symphytognathidae	1	—	—	1	—	—
Telemidae	1	—	—	3	—	—
Tengellidae	1	—	—	5	—	—
Theridiidae	27	6	22	231	7	3
Theridiosomatidae	1	1	100	2	1	50
Thomisidae	10	7	70	128	11	9
Uloboridae	7	2	29	15	2	13
Zodariidae	2	—	—	4	—	—
Zoridae	1	—	—	1	—	—
Totals	469	133	28.4	3311	234	7.1

Table 4.—Comparison of spider guilds, North America and Washington County, Mississippi. Each family assigned to a guild based on data from Roth (1985), Kaston (1981), Gertsch (1979), and Comstock (1940).

	Web-spinning	%	Wandering	%
N.A. Fauna				
No. Families	25	52	23	48
No. Genera	307	65	162	35
No. Species	1955	59	1356	41
Wash. Co.				
No. Families	11	42	15	58
No. Genera	51	38	82	62
No. Species	78	33	156	67

species. There is little doubt that areas of similar size to Washington County that had a more diversified range of habitats would have substantially more species in a larger set of genera and families.

It is also possible to compare certain functional aspects of the North American and Washington County faunas. By the use of such sources as Roth (1985), Kaston (1981), Gertsch (1979), and Comstock (1940), each spider family can be designated as composed primarily of either web-spinning or wandering species. The North American fauna at the species level is thus estimated to be 59% web-spinners and 41% wanderers (Table 4). The Washington County fauna, however, is estimated to include 33% web-spinners and 67% wanderers. The considerable differences between these estimates probably are due to the preponderance of disturbed habitats in Washington County and to the negative effect of habitat disturbance (destruction, loss) on web-spinning spider populations.

Comparison with other faunal surveys.—Spider faunal surveys were reviewed to compare with our efforts in Washington County. Spider faunal lists can be classified in the following categories: a) specific plant association, e.g., peppermint (McIver and Belnavis 1986), daisy (Judd 1965); b) specific habitat, e.g., tree-bark (Bower and Snetsinger 1985), salt-marsh (LaSalle and Cruz 1985); c) general habitat type, e.g., old-field communities (Berry 1970), broomsedge communities (Barnes and Barnes 1955); d) multi-habitat natural area, e.g., Itasca St. Park (Heimer et al. 1984), Univ. Kansas Natur. Hist. Res. (Fitch 1963); e) restricted geographic area such as a town (Brown 1974) or island (Drew 1967); f) county (Dorris 1968); g) multi-county (Branson and Batch, 1970); h) state or providence, e.g., Wisconsin (Levi and Field 1954), British Columbia (West et al. 1984); i) multi-state, e.g., Georgia area (Chamberlin and Ivie 1944).

An examination of this literature showed few previous surveys in common with our county-wide study. The one survey that covered a single county was merely a checklist of the species, with no additional data (Dorris 1968). The 108 species in the Dorris study were collected in one year by sweepnet, sifting of litter, and hand-picking, all in unspecified habitats. Two multi-county studies, from northwest Iowa (Abraham 1987) and northern Kentucky (Branson and Batch 1970), were of limited comparative value. The Iowa study listed only the genera, but claimed 154 species. The Kentucky study listed 85 species, but was based on only 503 specimens obtained by limited collecting. An attempt to extract county data from state lists was not productive. Most state lists contained county records, but very little information on habitats, seasonality, abundance, or

sampling methods [e.g., Maryland (Muma 1945), Nebraska (Worley and Pickwell 1927), Oklahoma (Banks et al. 1932), Texas (Vogel 1970), Washington (Worley 1932)]. Kaston's *magnus opus* on the spiders of Connecticut (1981) is certainly an exception to that statement, but unfortunately his data are not in a format that allows ready comparison with other faunal surveys.

Perhaps the only studies remotely comparable to the Washington County data involve multi-habitat natural areas and restricted geographic areas. The Itasca State Park (Minnesota) study of Heimer et al. (1984) listed 124 species, but did not indicate the size of the area sampled, the amount of sampling effort through time, the number of specimens examined, or detailed habitat information. A study from the University of Oklahoma Biological Station (Branson 1966) listed 83 species identified from ca 1000 specimens collected during four summers, but did not indicate the area sampled, contained little ecological data or analysis, and was essentially a key to the genera of Oklahoma spiders. The most thorough study of a natural area was that of Fitch (1963) at the 300 ha University of Kansas Natural History Reservation. This study was conducted over a 13 year period utilizing most sampling techniques, during all months of the year, and in a variety of microhabitats within the tall-grass prairie and deciduous woodland habitats. Of the 192 species listed, 119 (62%) were considered to be characteristic of a deciduous forest habitat and 56 (29%) were associated with grasslands. Within the woodlands, 85 species (71%) were obtained from leaf-litter and 29 (24%) from arboreal situation. This compares with 47% of the Washington County species collected from the ground strata and 70% from above-ground sites (all habitats combined, some species occurring in several strata).

Several studies that involve restricted geographic areas may be appropriate for comparison. Brown (1974) reported 147 species of spiders collected over a six-month period from Nacogdoches, Texas, and vicinity. This check-list contained no information on the area sampled and no analysis, but did indicate that the families Salticidae (30 spp.) and Araneidae (29 spp.) represented most of the species. In Washington County, these two families also were highly represented (Salticidae—47 spp., Araneidae—39 spp.). Perhaps the most defined geographic area that has been examined for spiders is Beaver Island in Lake Michigan (Drew 1967). This 15,000 ha island is 24 km from the nearest mainland and has a well-documented flora and fauna. Spiders were collected day and night in a variety of habitats over a four-year period by sweepnet, sifting, beating, and hand. Of the 211 species obtained, 54% were web-spinners and 46% were wanderers. In Washington County, 33% of 234 species were web-spinners and 67% were wanderers. Web-spinners are characteristic of undisturbed sites containing adequate web supports (Duffey 1978), and their comparatively low incidence in Washington County could be due to the overwhelming predominance of disturbed habitats.

Comparison of various characteristics of the Washington County spider fauna with data from other faunal surveys has clearly indicated that the Washington County fauna is disproportionately well-represented by species typical of disturbed habitats. Some species, such as *Oxyopes salticus*, *Tetragnatha laboriosa*, and *Pardosa milvina*, may develop high population densities in habitats adjacent to crop fields. Crop insect pests occupying these habitats are probably exposed to considerable predation by spiders. Management of these habitats to conserve and enhance spiders and other predators could have a significant effect on crop pest populations.

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APPENDIX

SPIDERS OF WASHINGTON COUNTY, MISSISSIPPI, 1981-87.

Explanation of symbols.—*Month Collected:* Each month is designated by its first letter and is listed in chronological sequence. A dash between letters indicates that all intervening months not listed contained specimens of that species. A blank space between letters indicates that no specimens were found in the unlisted months. When certain months are listed alone, a second letter is added to avoid confusion: Ja = January, Je = June, Jy = July, Mr = March, My = May, Ap = April, Au = August.

Habitat: F = forest, T = transitional area between forest and field or road, C = crop field, M = meadow or grassland, O = old-field in early successional state 2-5 years after plowing, W = water margin such as edge of pond, stream, or drainage ditch, R = road or field margin, L = lawn in residential area, B = building, S = spanish moss hanging from trees 2-5 m above ground.

Strata: G = ground, H = herbs and grass 0.5-2.0 m above ground, S = shrubs 1-4 m above ground, T = tree 3-5 m above ground.

Abundance (Ab): A = abundant, C = common, U = uncommon, R = rare. Each species was assigned an abundance designation after a review of all collection records from the seven-year period and, although quite subjective, is our best estimate in the absence of quantitative data.

Capture method: P = pitfall trap, S = sweepnet, V = vacuum device, H = hand.

State Record (St Rc): Asterisk indicates addition to state list of Dorris (1972).

Taxon	Month coll.	Habitat	Strata	Ab	Capture	St Rc
AGELENIDAE						
<i>Agelenopsis naevia</i> (Walck.)	JJASO	TMOR	GHS	A	SVH	
<i>Agelenopsis utahana</i> (Chamb. & Ivie)	Jy	O	H	R	P	*
<i>Coras medicinalis</i> (Hentz)	Ja D	OR	G	C	PV	
ANYPHAENIDAE						
<i>Anyphaena celer</i> (Hentz)	JFMA SOND	FO	GH	U	PV	
<i>Anyphaena maculata</i> (Banks)	FMAM SOND	S	T	A	HB	*
<i>Anyphaena</i> sp. A	My	OR	H	R	PS	
<i>Aysha gracilis</i> (Hentz)	My	R	H	R	S	
<i>Teudis mordax</i> (O.P.-Cambridge)	MJ	R	H	R	SB	*
<i>Wulfila</i> sp.	AM S	O	GH	R	SV	*
ARANEIDAE						
<i>Acacesia hamata</i> (Hentz)	Au	O	S	R	S	*
<i>Acanthepeira stellata</i> (Walck.)	M JJASON	FTORC	HST	C	SVH	
<i>Alpaida calix</i> (Walck.)	MJ	O	H	R	V	
<i>Araneus cingulatus</i> (Walck.)	Jy	O	H	R	V	*
<i>Araneus marmoreus</i> Clerck	S	T	T	U	H	
<i>Araneus miniatus</i> (Walck.)	Je S	T	S	U	H	
<i>Araneus pratensis</i> (Emerton)	Au	T	T	U	H	
<i>Araneus</i> sp. A	Jy	TC	H	R	S	
<i>Argiope aurantia</i> Lucas	ASON	TCOR	HST	C	SH	
<i>Argiope trifasciata</i> (Forskål)	AS	O	H	R	H	
<i>Colphepeira catawba</i> (Banks)	J—D	O	H	U	SV	*
<i>Cyclosa conica</i> (Pallas)	Je	R	H	R	S	
<i>Cyclosa turbinata</i> (Walck.)	My	R	H	R	S	
<i>Eustala cepina</i> (Walck.)	Ja AM	OSM	HT	R	VB	*
<i>Eustala</i> sp. A	My	O	H	R	S	*
<i>Gasteracantha cancriformis</i> (L.)	Ja JASOND	TO	ST	C	SH	
<i>Gea heptagon</i> (Hentz)	AMJJA	CMOR	GH	C	SV	*
<i>Glenognatha foxi</i> (McCook)	AMJJAS	CMORL	GH	C	PSV	*
<i>Hypsosinga</i> sp.	Ap	O	H	R	S	*
<i>Leucauge venusta</i> (Walck.)	MJJ	FTCR	HS	C	SH	
<i>Mangora</i> sp.	O	O	H	R	S	
<i>Mastophora phrynosoma</i> Gertsch	O	T	T	R	H	*
<i>Metazygia wittfeldae</i> (McCook)	Je	R	H	R	S	*
<i>Micrathena gracilis</i> (Walck.)	JJ	F	ST	C	H	

<i>Micrathena mitrata</i> (Hentz)	Jy	F	ST	U	H	*
<i>Micrathena sagittata</i> (Walck.)	Jy	F	ST	U	H	
<i>Neoscona arabesca</i> (Walck.)	MJJAS	CMORW	HS	A	SVH	
<i>Neoscona domiciliorum</i> (Hentz)	My J	TCRS	HST	U	SB	
<i>Neoscona hentzii</i> (Keys.)	AS	TCWRS	HST	C	SB	*
<i>Neoscona nautica</i> (L. Koch)	SO	T	T	U	H	*
<i>Neoscona pratensis</i> (Hentz)	AS	TC	T	U	S	*
<i>Nuctenea</i> sp.	O	O	H	R	S	*
<i>Pachygnatha</i> sp.	A JJA	CO	GH	C	PS	
<i>Tetragnatha elongata</i> Walck.	AMJJAS	COR	HS	C	SV	*
<i>Tetragnatha laboriosa</i> Hentz	AMJJASO	TCOWR	HS	A	SVH	
<i>Tetragnatha straminea</i> Emerton	AMJJAS	COWR	HS	U	SV	
<i>Tetragnatha versicolor</i> Walck.	AMJJASO	TCOR	HS	C	SV	
<i>Verrucosa arenata</i> (Walck.)	Au	F	ST	U	H	
<i>Wixia</i> sp.	AM J	COR	H	R	SV	
ATYPIDAE						
<i>Sphodros bicolor</i> (Lucas)	A Je	F	G	R	P	*
CLUBIONIDAE						
<i>Agroeca pratensis</i> Emerton	Jy	L	G	R	P	
<i>Castianeira gertschi</i> Kaston	S	O	GH	R	SV	
<i>Castianeira longipalpus</i> (Hentz)	Ap N	O	GH	U	SV	
<i>Chiracanthium inclusum</i> (Hentz)	JJA	CO	H	R	S	
<i>Clubiona abbotii</i> L. Koch	AMJ ON	O	H	C	SV	
<i>Clubiona obesa</i> Hentz	AMJ	O	H	U	SV	
<i>Clubionoides</i> sp.	F AMJJAS	TCRS	HT	U	SB	*
<i>Phrurotimpus</i> sp.	A J AS	FOR	GH	C	PV	*
<i>Scotinella</i> sp.	Je	R	H	R	S	*
<i>Trachelas deceptus</i> (Banks)	JA	B	G	C	H	*
<i>Trachelas similis</i> F.O.P.-Cambridge	Jy	R	H	R	S	*
<i>Trachelas tranquillus</i> (Hentz)	Au	O	G	R	P	
<i>Trachelas</i> sp. A	Jy	R	H	U	S	
DICTYNIDAE						
<i>Dictyna hentzi</i> Kaston	AMJ	OR	GH	U	PSV	*
<i>Dictyna</i> sp. A	AM	OR	GH	U	PSV	
DYSDERIDAE						
<i>Dysdera crocata</i> C. L. Koch	Ap	F	G	R	P	
FILISTATIDAE						
<i>Filistata hibernalis</i> Hentz	J—N	B	G	C	H	
GNAPHOSIDAE						
<i>Callilepis imbecilla</i> Keys.	My S	OR	H	U	PS	
<i>Cesonia bilineata</i> (Keys.)	Ap	S	T	R	B	
<i>Drassodes gosiutus</i> Chamb.	Au	O	G	R	P	*
<i>Drassyllus aprilius</i> (Banks)	My	O	G	R	P	*
<i>Drassyllus covensis</i> Exline	My	O	G	R	P	*
<i>Drassyllus creolus</i> Chamb. & Gertsch	My	O	G	R	P	*
<i>Drassyllus dixinus</i> Chamb.	My	O	G	R	P	*
<i>Drassyllus ellipes</i> Chamb. & Gertsch	Je	O	G	R	P	*
<i>Drassyllus gynosaphes</i> Chamb.	AMJ A	FTO	G	C	P	*
<i>Drassyllus lepidus</i> (Banks)	Jy	O	G	R	P	*
<i>Drassyllus novus</i> (Banks)	My	O	G	R	P	*
<i>Gnaphosa fontinalis</i> Keys.	JJA	OR	GH	C	PS	*
<i>Gnaphosa sericata</i> (L. Koch)	Au	O	G	U	P	
<i>Haplodrassus signifer</i> (C. L. Koch)	My	R	H	R	S	
<i>Herpyllus ecclesiasticus</i> Hentz	AM A O	B	G	C	H	*
<i>Micaria delicatula</i> Bryant	AM ON	FO	GH	U	PV	*
<i>Nodocion floridanus</i> (Banks)	MAMJ D	S	T	C	B	*
<i>Sergiolus capulatus</i> (Walck.)	Je	O	G	R	P	*
<i>Sergiolus minutus</i> (Banks)	My	O	G	R	P	*
<i>Sergiolus ocellatus</i> (Walck.)	Je O	O	G	U	PV	*

<i>Urozelotes rusticus</i> (L. Koch)	Ap	O	G	R	P	*
<i>Zelotes aiken</i> Platnick & Shadab	My	T	G	R	P	*
<i>Zelotes duplex</i> Chamb.	AM	TO	G	U	P	*
<i>Zelotes hentzi</i> Barrows	MAM	OR	GH	U	PS	
<i>Zelotes laccus</i> (Barrows)	AM	R	G	C	P	*
HAHNIIDAE						
<i>Hahnina cinerea</i> Emerton	J MAM D	FO	G	C	PV	*
<i>Hahnina flaviceps</i> Emerton	AM	O	G	R	P	*
<i>Neoantistea agilis</i> (Keys.)	N	O	G	U	V	*
LINYPHIIDAE						
<i>Ceraticelus emertoni</i> (O.P.-Camb.)	J—D	TCMORL	GH	A	PSVB	*
<i>Ceraticelus</i> sp. A	My	O	G	U	P	
<i>Eperigone</i> sp. A	AM	R	G	U	P	*
<i>Eperigone</i> sp. B	AM	R	G	U	P	
<i>Eperigone</i> sp. C	Ap	R	G	R	P	
<i>Erigone</i> sp. A	AM	R	G	U	P	*
<i>Erigone</i> sp. B	My	R	G	R	P	
<i>Floricomus</i> sp. A	AM	R	G	U	P	*
<i>Floricomus</i> sp. B	Ap	R	G	R	P	
<i>Florinda</i> sp.	AM	R	GH	U	PS	*
<i>Frontinella pyramitela</i> (Walck.)	J M Je D	O	H	C	S	
<i>Grammonota</i> sp. A	AM	R	GH	C	PS	*
<i>Grammonota</i> sp. B	Ap	R	G	R	P	
<i>Linyphia</i> sp.	AMJ	OR	H	U	S	
<i>Meioneta</i> sp.	AM	R	G	R	P	*
<i>Neriere radiata</i> (Walck.)	JJA	COR	H	C	SV	
<i>Pityohyphantes</i> sp.	My	R	G	R	P	*
LOXOSCELIDAE						
<i>Loxosceles reclusa</i> Gert. & Mul.	J JJA ON	B	G	U	H	
<i>Loxosceles rufescens</i> (Dufour)	F AS	B	G	R	H	*
LYCOSIDAE						
<i>Allocosa absoluta</i> (Gertsch)	AMJ	R	G	C	P	*
<i>Allocosa funerea</i> (Hentz)	F AMJJ	ORL	G	C	P	
<i>Allocosa</i> sp. A	Ap	R	G	R	P	
<i>Arctosa littoralis</i> (Hentz)	Je A	OR	G	U	PS	
<i>Gladicosa bellamyi</i> (Gert. & Wall.)	AMJJA	T	G	C	P	*
<i>Gladicosa gulosa</i> (Walck.)	J—N	FTO	G	A	PH	*
<i>Gladicosa pulchra</i> (Keys.)	JFMA S ND	FL	G	R	P	*
<i>Lycosa acompa</i> Chamberlin	FM MJ N	OL	G	C	PH	*
<i>Lycosa annexa</i> Chamb. & Ivie	J-J A-D	FTORLB	G	A	PH	*
<i>Lycosa aspersa</i> Hentz	MJ	TO	G	R	P	
<i>Lycosa antelucana</i> Montgomery	A J A	OL	H	R	PH	
<i>Lycosa baltimoriana</i> (Keys.)	S	O	G	R	P	
<i>Lycosa carolinensis</i> Walck.	O	O	G	R	P	
<i>Lycosa georgicola</i> Walck.	J AMJJASON	FTO	G	U	PH	*
<i>Lycosa helluo</i> Walck.	MJJ	FT	G	C	PH	
<i>Lycosa helluo</i> group	MJJAS	CR	GH	C	H	
<i>Lycosa lenta</i> (Hentz)	J—D	COR	G	C	PH	
<i>Lycosa lenta</i> group	MJJAS	CR	GH	A	H	
<i>Lycosa punctulata</i> Hentz	AM SON	TRO	GH	U	PH	
<i>Lycosa rabida</i> Walck.	MJJAS N	CMORL	HS	A	SH	
<i>Pardosa atlantica</i> Emerton	AM	R	GH	U	PS	*
<i>Pardosa milvina</i> (Hentz)	J—D	FTCMOWRL	GHS	A	PSVH	
<i>Pardosa saxatilis</i> (Hentz)	MJ A	MOR	GH	C	PS	
<i>Pirata insularis</i> Emerton	AMJJA	MOR	GH	C	PS	
<i>Pirata minutus</i> Emerton	J AMJ N	OR	GH	U	PSV	*
<i>Pirata</i> sp. A	JJ	O	G	R	P	
<i>Schizocosa avida</i> (Walck.)	AMJJASOND	FTMORL	GH	A	PVH	
<i>Schizocosa humilis</i> (Banks)	S	O	G	R	P	*

<i>Schizocosa ocreata</i> (Hentz)	AMJJASOND	FTOL	GH	C	PH	
<i>Sosippus mimus</i> Chamb.	F	F	G	R	H	*
<i>Trabeops aurantiaca</i> (Emerton)	F AMJJAS	FTOR	GH	U	PS	*
<i>Trochosa avara</i> Keys.	F—D	FTO	G	U	PS	
MIMETIDAE						
<i>Mimetus</i> sp.	Ap D	RS	T	R	HB	
NESTICIDAE						
<i>Nesticus</i> sp.	MJ	O	H	R	P	*
OECOBIIDAE						
<i>Oecobius</i> sp.	My JA	B	G	R	H	*
OONOPIDAE						
<i>Orchestina saltitans</i> Banks	MJ	B	G	R	H	*
OXYOPIDAE						
<i>Oxyopes salicus</i> Hentz	AMJJASON	TCMOWRL	HS	A	PSVH	
<i>Peucetia viridans</i> (Hentz)	Jy	F	S	R	S	
PHILODROMIDAE						
<i>Ebo latithorax</i> Keys.	MAMJ AS ND	FTOR	H	U	SV	
<i>Philodromus keyserlingi</i> Marx	AM	O	G	R	VB	*
<i>Philodromus marxi</i> Keys.	AMJJASO	TORS	GHST	C	PSV	*
<i>Philodromus placidus</i> Banks	MJ	T	S	R	S	*
<i>Philodromus vulgaris</i> (Hentz)	My	S	T	R	B	*
<i>Tibellus duttoni</i> (Hentz)	AMJJAS	TOR	HS	A	SVH	*
<i>Tibellus oblongus</i> (Walck.)	Jy	R	H	R	S	
PHOLCIDAE						
<i>Pholcus phalangoides</i> (Fues.)	J—D	B		C	H	
<i>Psilochorus</i> sp.	Jy	CR	H	R	S	*
<i>Spermophora meridionalis</i> Hentz	AM	B		R	H	
PISAURIDAE						
<i>Dolomedes iriton</i> (Walck.)	MAMJJASON	TMOWR	GH	A	PSVH	
<i>Pisaurina mira</i> (Walck.)	AMJJA ON	TCOWRL	GHS	A	PSVH	
<i>Pisaurina undulata</i> (Keys.)	J—D	FMOR	HS	A	SVH	
<i>Tinus peregrinus</i> (Bishop)	O	O	H	R	S	
SALTICIDAE						
<i>Agassa cyanea</i> (Hentz)	Mr—D	TMOR	GH	C	PSV	
<i>Ballus cinctipes</i> (Banks)	Je	O	H	R	S	*
<i>Ballus</i> sp. A	AS	OW	H	R	SV	
<i>Corythalia canosa</i> (Walck.)	Je	B		R	H	*
<i>Corythalia latipes</i> C. L. Koch	Ap	O	G	R	P	*
<i>Eris aurantia</i> (Lucas)	Jy	O	HS	U	S	
<i>Eris militaris</i> (Hentz)	M MJJASO	TCMORS	HST	C	SB	
<i>Euophrys</i> sp.	Jy	O	H	R	S	*
<i>Evarcha hoyi</i> (Peckhams)	AMJJASO	OR	H	C	SV	
<i>Habrocestum pulex</i> (Hentz)	Je S	FO	GH	U	PS	
<i>Habronattus agilis</i> (Banks)	MJJASO	MOR	HS	C	PSV	
<i>Habronattus calcaratus</i> (Banks)	Jy	O	S	R	S	*
<i>Habronattus coecatus</i> (Hentz)	AMJJASO	MOWR	GH	A	PSV	
<i>Habronattus decorus</i> (Blackwall)	Au	CW	H	U	H	
<i>Hentzia mīrata</i> (Hentz)	JF Au	RS	HT	R	SB	
<i>Hentzia palmarum</i> (Hentz)	JJ	CR	H	U	S	
<i>Maevia inclemens</i> (Walck.)	MJ S	OWB	H	C	SH	
<i>Marpissa bina</i> (Hentz)	Je	O	HS	U	S	
<i>Marpissa formosa</i> (Banks)	AM	O	H	U	S	*
<i>Marpissa lineata</i> (C. L. Koch)	Mr	O	H	R	S	*
<i>Marpissa pikei</i> Peckhams	S	O	H	U	S	
<i>Metacyrba taeniola</i> (Hentz)	A JJ	O	HS	U	HS	
<i>Metaphidippus galathea</i> (Walck.)	F Ap—N	TCMOWR	HS	A	S	
<i>Metaphidippus protervus</i> (Walck.)	AMJJASO	OR	HS	C	S	
<i>Metaphidippus tillandsiae</i> Kaston	JFMAM OND	S	T	C	B	*
<i>Neon nelli</i> Peckhams	ASO	TOR	H	R	S	

<i>Neonella vinnula</i> Gertsch	Au	R	H	R	S	*
<i>Phidippus audax</i> (Hentz)	Ap—D	COW	HST	A	SH	
<i>Phidippus clarus</i> Keys.	MJJASON	CO	HS	A	SH	
<i>Phidippus insignarius</i> C. L. Koch	S	O	HS	U	S	*
<i>Phidippus otiosus</i> (Hentz)	MJ S	O	S	R	S	
<i>Phidippus princeps</i> Peckhams	Jy	O	S	R	S	
<i>Phidippus purpuratus</i> Keys.	Je	O	S	U	S	
<i>Phidippus putnami</i> (Peckhams)	S D	S	T	R	B	*
<i>Phlegra fasciata</i> (Hahn)	Au	O	S	R	S	
<i>Platycryptus undatus</i> (DeGeer)	JJAS	WBS	HT	U	SHB	
<i>Plexippus paykulli</i> (Audouin)	SO	O	H	R	S	*
<i>Sarinda</i> sp.	Jy	O	H	R	S	*
<i>Sassacus papenhoei</i> Peckhams	N	O	H	R	S	
<i>Sitticus cursor</i> Barrows	AMJ	O	HS	R	S	*
<i>Thiodina puerpera</i> (Hentz)	MJ O	FO	H	C	S	
<i>Thiodina sylvana</i> (Hentz)	MJJASO	CO	HS	U	S	
<i>Tutelina elegans</i> (Hentz)	JJASO	CO	HS	U	S	
<i>Tutelina similis</i> (Banks)	My	R	H	U	S	*
<i>Zygoballus nervosus</i> (Peckhams)	My D	OS	HT	U	HB	
<i>Zygoballus rufipes</i> Peckhams	AMJJ SOND	MO	GHS	C	SV	*
<i>Zygoballus sexpunctatus</i> (Hentz)	AMJ ASO D	OW	GH	U	V	
SCYTODIDAE						
<i>Scytodes thoracica</i> (Latr.)	J—D	B	G	U	H	
THERIDIIDAE						
<i>Achaearanea globosa</i> (Hentz)	JJ SO	B	G	R	H	*
<i>Achaearanea tepidariorum</i> (C. L. Koch)	J—D	B	G	A	H	
<i>Euryopsis funebris</i> (Hentz)	My	S	T	R	B	
<i>Latrodectus mactans</i> (F.)	J—D	CMOB	GH	U	H	
<i>Steatoda</i> sp.	JJA	OR	H	U	S	*
<i>Theridion frondeum</i> Hentz	MJJASO	TMOR	GH	U	PSV	
<i>Theridula opulenta</i> (Walck.)	MJJAS	MOR	GH	U	PSV	*
THERIDIOSOMATIDAE						
<i>Theridiosoma gemmosum</i> (L. Koch)	Mr AS D	COR	GH	R	PSV	
THOMISIDAE						
<i>Coriarachne</i> sp.	AM	OR	H	R	SV	
<i>Misumena vatia</i> (Clerck)	MJJAS	TCOR	HS	C	SH	
<i>Misumenoides formosipes</i> (Walck.)	JJASON	TCOR	HS	C	SH	
<i>Misumenops asperatus</i> (Hentz)	JJAS	TCOR	HS	U	S	
<i>Misumenops celer</i> (Hentz)	JJA	COR	H	U	S	
<i>Misumenops oblongus</i> (Keys.)	MJJ S	OR	H	U	S	*
<i>Oxyptila monroensis</i> Keys.	AMJ OND	FO	G	C	PS	*
<i>Synaema parvula</i> (Hentz)	JA	CO	H	U	S	
<i>Xysticus ferox</i> (Hentz)	AMJJAS	FOR	GH	C	PS	
<i>Xysticus fraternus</i> Banks)	AMJJAS	FO	G	C	PS	*
<i>Xysticus triguttatus</i> Keys.	Je	F	G	R	P	
ULOBORIDAE						
<i>Uloborus</i> sp.	MA JJAS	TO	HS	U	SV	
<i>Zosis geniculatus</i> (Olivier)	Jy	O	S	R	S	

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**PREDATION BY *PISAUURINA MIRA* (ARANEAE, PISAURIDAE)
ON *LYGUS LINEOLARIS* (HETEROPTERA, MIRIDAE)
AND OTHER ARTHROPODS**

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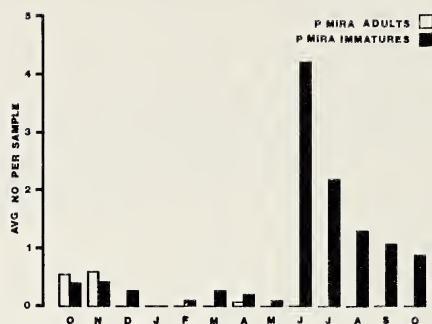
ABSTRACT

In the Delta area of Mississippi, a 13-month sampling program in old-field habitats adjacent to cotton fields demonstrated high densities of *Pisaurina mira* in June, which was coincident with high *Lygus lineolaris* populations. In July, *P. mira* populations were lower by 50% and *L. lineolaris* by almost 100%. From August through October, *P. mira* populations continued to decline while *L. lineolaris* increased. Field observations in the same old-field habitats indicated *L. lineolaris* to be the most frequently captured prey item of *P. mira*. In laboratory feeding experiments over a 3-year period, all *P. mira* individuals consumed *L. lineolaris* and 22 of 35 other species of co-occurring potential arthropod prey. These data suggest that the predator *P. mira* may affect *L. lineolaris* populations and can survive on other prey when *L. lineolaris* is less abundant.

INTRODUCTION

Members of the Pisauridae in North America are wandering spiders that do not build snares and are typically found on vegetation or at water margins throughout North America (Carico 1972). *Pisaurina mira* (Walckenaer) is one of the most common spiders in the eastern United States and occurs in woods, old-fields, and meadows, but is especially abundant in the ecotonal areas between woods and fields (Carico 1972). This species can be an important predator in row crops and has been recorded from rice (Woods and Harrel 1976), sugarcane (Negm et al. 1969), peanuts (Agnew et al. 1985), soybeans (LeSar and Unzicker 1978), cotton (Whitcomb and Bell 1964), and alfalfa (Wheeler 1973). *P. mira* has been documented recently in the laboratory as a voracious predator on the tarnished plant bug (TPB), *Lygus lineolaris* (Palisot) (Heteroptera, Miridae) (Young 1989). The TPB is an economically important pest on many crops in the United States, feeds on over 350 species of plants, and is abundant in habitats adjacent to row crops (Young 1986). Since these are the same habitats in which *P. mira* is abundant, it is possible that this spider could have a significant impact on TPB populations. The purpose of this study was to delineate the seasonal populations of *P. mira* in field edge habitats, and to determine which arthropods were present in those same habitats which *P. mira* could feed upon.

Figure 1.—Average number per sample of *Pisaurina mira* adults and immatures for each of 13 consecutive months in old-field habitats adjacent to cotton fields in Washington County, Mississippi.



METHODS AND MATERIALS

Field.—Arthropods were collected by sweepnet and/or vacuum (D-vac®), 10 sweeps or 10 row-feet per sample, at 15 undisturbed early-successional sites adjacent to cotton fields in Washington County, Mississippi. Sampling was conducted on alternate weeks during the period October 1985 through October 1986. All *P. mira* and potential prey were removed from the samples, counted, and determined as to immature or adult. On an irregular basis throughout the 13-month period, observations of *P. mira* predation on various prey at these same sites were recorded.

Laboratory.—Individuals of *P. mira*, obtained from the above-mentioned and other similar sites during 1984-86, were placed in plastic cups (4 by 10 cm) with a cloth-mesh cover and maintained in an environmental chamber at 25°C, 80% RH, and a 14:10 (L:D) photoperiod. The feeding protocol involved starving (water available) each spider for the seven days after capture, placing an individual live prey in each container, recording the prey status after 24 hours, and removing the unconsumed material. Spiders not consuming prey were offered one adult TPB, which was always accepted. The starvation—feeding—recording cycle was then repeated several times for each spider using different potential prey in each cycle. These feeding trials were conducted during the late summer and fall of 1984-1986, with both *P. mira* and potential prey collected from the same sites. Each potential prey species was offered to 3-10 different spiders, depending upon availability of the prey.

RESULTS AND DISCUSSION

Seasonal occurrence.—During the 13-month sampling period, 44 adult *P. mira* were captured, with 98% occurring in October and November (Fig. 1). Three-hundred and seventy immatures were also captured, with the largest number (40%) occurring in June. These patterns of occurrence indicate that adults and late-instar immatures overwinter, that eggs hatch in May with dispersal of immatures from nursery webs in June, and that *P. mira* is univoltine. Published information from other collection sites indicate a similar pattern. Adults of *P. mira* are most abundant during June in Illinois (Jones 1940), Kansas (Fitch 1963), and Tennessee (Gibson 1947), and during May in North Carolina (Berry 1971) and Arkansas (Peck et al. 1971). Immatures were most abundant during

Table 1.—Field observations of prey capture by *Pisaurina mira*.

Prey taxon	Prey stage	No. observations
Heteroptera: Miridae		
<i>Lygus lineolaris</i> (Palisot)	Adult	2
<i>L. lineolaris</i>	Immature	3
<i>Polymerus basalıs</i> (Reuter)	Adult	1
Homoptera: Cicadellidae, Undet. sp.	Immature	2
Coleoptera: Chrysomelidae		
<i>Diabrotica undecimpunctata howardi</i> Barber	Adult	2
Diptera: Muscidae, Undet. sp.	Adult	1
Hymenoptera: Apidae		
<i>Apis</i> sp.	Adult	1

September in Ohio (Elliott 1930) and Tennessee (Gibson 1947), during August in North Carolina (Berry 1971) and Kansas (Fitch 1963), and abundant throughout the June to October period in Illinois (Jones 1940) and Arkansas (Peck et al. 1971). Mississippi populations appear to develop earlier than those further north, but there is no evidence for a second generation.

Field observations of predation.—A survey of the spider literature revealed an absence of records involving prey of *P. mira*. Considering the dense and low vegetation in which this species is most abundant, perhaps the lack of prey records is not surprising. During several hundred hours of field work over a 13-month period, only 12 *P. mira* with prey were recorded (Table 1). The species captured were among the most abundant species present at the time of the observations. Five of the 12 prey records (43%) involved the TPB, and since the TPB comprised considerably less than 43% of the arthropod population (Young unpubl. data), it is possible that *P. mira* demonstrated some specificity for the TPB.

Laboratory observations.—Over a 3-year period, 41 individuals of *P. mira* were offered 36 species of prey representing 22 families of insects in eight orders and three families of spiders (Table 2). Not all of these potential prey were captured and consumed, as 77 of the 179 specimens were rejected (43%). Thirteen species (56 individuals) were completely rejected by *P. mira*. Situations in which the potential prey was as large or larger than the spider, or considerably smaller, usually resulted in an absence of prey capture, as did the presence of probable

Table 2.—Laboratory observations of prey capture by *Pisaurina mira*.

Prey taxon	Prey life state	Prey mean body length (mm)	<i>P. mira</i> mean body length (mm)	Prey consumed	
				Yes	No
COLEOPTERA					
Carabidae					
<i>Lebia viridis</i> (Say)	Ad	5	5	6	
Coccinellidae					
<i>Cycloneda munda</i> (Say)	Ad	5	6		4
<i>Hippodamia convergens</i> Guerin	Ad	6	7		8
Chrysomelidae					
<i>Diabrotica undecimpunctata howardi</i> Barber	Ad	7	9	2	3

DIPTERA

Syrphidae, Undetermined species	Ad	6	6	4
Calliphoridae, Undet. sp.	Ad	6	7	3

HEMIPTERA

Coreidae, Undet. sp.	Imm	14	10	4	
Lygaeidae					
<i>Blissus</i> sp.	Ad	3	7	2	5
<i>Geocoris punctipes</i> Say	Ad	4	5	6	2
<i>Oncopeltis</i> sp.	Ad	15	8		3
<i>Oncopeltis</i> sp.	Imm	8	9	2	
Miridae					
<i>Lygus lineolaris</i> (Palisot)	Ad	5	7	10	
<i>Taylorilygus pallidulus</i> Blanchard	Ad	4	6	5	
Nabidae					
<i>Reduviolus roseipennis</i> (Reuter)	Ad	7	8		4
<i>Tropiconabis capsiformis</i> (Gemar)	Ad	8	7	1	2
Pentatomidae					
<i>Stiretrus anchorago</i> (F.)	Ad	8	7	1	2
Reduviidae					
<i>Sinea diadema</i> (F.)	Ad	13	10		3
<i>Zelus</i> sp.	Imm	12	13		6

HOMOPTERA

Cicadellidae					
<i>Chlorotettix</i> sp.	Ad	5	7	6	
<i>Gyponana</i> sp.	Ad	5	9	3	
Fulgoridae, Undet. sp.	Ad	8	9		2
Membracidae					
<i>Spissistilus festinus</i> (Say)	Ad	5	8		6

HYMENOPTERA

Halictidae					
<i>Augochlor</i> sp.	Ad	5	7	6	
Undet. sp.	Ad	8	13	3	

LEPIDOPTERA

Geometridae, Undet. sp.	Imm	11	10	4
Noctuidae				
<i>Heliothis</i> sp.	Imm	7	7	6
<i>Spodoptera</i> sp.	Imm	7	7	6
Syntomidae				
<i>Ctenucha</i> sp.	Ad	9	9	3
Yponomeutidae				
<i>Atteva</i> sp.	Ad	10	8	4

NEUROPTERA

Chrysopidae					
<i>Chrysopa</i> sp.	Imm	6	6		5

ORTHOPTERA

Acrididae, Undet. sp.	Ad	8	8	3	
Tettigoniidae					
<i>Neoconocephalus</i> sp.	Imm	5	7	5	

ARANEAE

Oxyopidae					
<i>Oxyopes salticus</i> Hentz	Imm	4	8	8	
Salticidae					
<i>Metaphidippus</i> sp.	Imm	3	9	3	3
<i>M. galathea</i> (Walck.)	Ad	4	6	5	4
<i>Phidippus</i> sp.	Imm	6	9	4	
Thomisidae					
<i>Misumenoides formosipes</i> (Walck.)	Imm	2	6		3

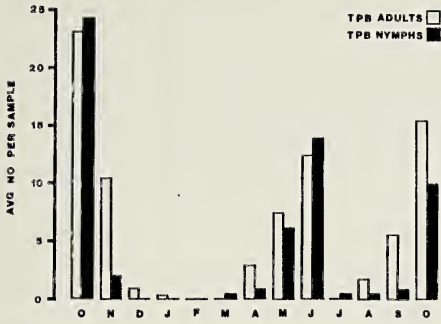


Figure 2.—Average number per sample of *Lygus lineolaris* adults and nymphs for each of 13 consecutive months in old-field habitats adjacent to cotton fields in Washington County, Mississippi.

distasteful prey (coccinellids and coreids). When the offered prey was also a predator, such as nabids or other spiders, prey capture sometimes did not occur. The size range of *P. mira* adults and juveniles utilized in these feeding trials was 5-13 mm body length and that of accepted prey was 4-14 mm. Twenty-three species were accepted as prey under these laboratory conditions, and four additional species were observed as prey in the field. These 27 prey species were among the most abundant arthropods at the sampled sites, suggesting that *P. mira* can capture most arthropod species on vegetation within a particular size range. It must be remembered, however, that all laboratory spiders were offered, and accepted, adult TPB at some time during their captivity.

Potential impact on TPB populations.—The seasonal distribution of TPB at the same sites from which *P. mira* was collected is presented in Fig. 2. Population peaks of TPB occur in October and June, with the June peak followed in July by a veritable absence of TPB. The population peak of *P. mira* was also in June (Fig. 1). This correspondence of high population levels in June indicates that the TPB was abundantly available as prey for *P. mira* at that time. Subsequent population decline of TPB in July (Fig. 2) may have been due to emmigration out of field margins into cotton and/or mortality due to predators such as *P. mira*. Field and laboratory observations also suggest that when TPB is abundant, *P. mira* will be a frequent predator of this prey, and when TPB is relatively scarce, *P. mira* can readily feed on other prey.

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NEST ACCEPTANCE BY THE CRAB SPIDER *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

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ABSTRACT

I tested whether female crab spiders *Misumena vatia* responded differently to their own nests and to other spider nests or parts of nests. They accepted nests of conspecifics as readily as their own, although initially showing more activity on others' nests than their own. They accepted intact *M. vatia* nests more often than nest silk placed on leaves, turned-under leaves, or artificial nests; and unaltered leaves less frequently than any of the latter. They accepted nests of other spider species less frequently than conspecific nests, probably in response to the differences between these nests and conspecific nests. Some crab spiders about to lay their eggs accepted conspecific nests, but hunting adult females did not accept them more than predicted by chance.

INTRODUCTION

Parental care has recently engendered considerable interest because of its importance to theories of parental investment (Trivers 1972), parent-young conflict (Trivers 1974) and life histories (Stearns 1976, 1977). Considerably less attention has been simultaneously paid to the proximal cues used by parents to identify their young or their nest-sites. Nevertheless, these cues are crucial to the success of parental strategies and are therefore demanding of attention. In the past such cues have been the subject of considerable attention in their own right as sign stimuli or releasers (e. g., Tinbergen 1951).

Parental care ranges from guarding eggs to caring for them and the resulting offspring until they approach reproductive maturity. The extent of this commitment depends in part on the ability of parents to perform a variety of acts, ranging from site tenacity to recognizing their own nests, and their predisposition to care for eggs or young (see Trivers 1974). Sometimes it is unclear whether parental care results from site tenacity or recognition, especially among invertebrates, including ones whose behavioral patterns might help to clarify the evolution of parental care and other types of sociality (Wilson 1975). Understanding the conditions, cues, and mechanisms associated with parental care in a broad range of animals is thus particularly desirable.

Here I provide the results of studies on nest recognition by the semelparous crab spider *Misumena vatia* (Clerck) (Thomisidae). Female crab spiders lay their single egg mass in a nest that they construct from a large ovate leaf. They build this nest by bending under the distal tip of the leaf and securing it to the under side of this leaf (mid-section). Eggs are laid on silk within the cavity produced,

and the lateral sides are then drawn tight (Morse 1985). They subsequently guard this nest, often until young have emerged from the nest nearly four weeks later and sometimes until all the young have dispersed from the nest, as much as 12 days after that time (Morse 1987). Guarding behavior enhances survival of the affected offspring (Morse in press).

These spiders seldom wander far from the nests during the guarding phase, and they usually are connected to their sites by a silken line, which would facilitate return. However, they occasionally become separated from their nests. These individuals do not appear to have abandoned the sites "intentionally", for they may assume guarding positions in similar locations on nearby plants ($N = 4$).

Misumena vatia can be readily removed from their nests for weighing at any time during the guarding period and then returned, without affecting their desertion rate (Morse 1987). This result suggested that they could be transferred to other selected substrates, most obviously nests of conspecifics, in order to compare their performance with those on their own nest sites.

In this paper I present the results of experiments designed to establish whether female crab spiders respond differently to their own nests and to other nests. Also I investigated several cues that may facilitate nest recognition. Specifically, I ask: 1) can crab spiders recognize their own nests, or 2) nests of their own species? 3) If so, what characteristics are crucial in their identifications? If not, to what cues do they respond that their nests have in common with other features of the environment?

METHODS

All of the post-laying *Misumena* used in this study constructed their nests on milkweed (*Asclepias syriaca* L.) leaves in a field in Bremen, Lincoln Co., Maine (see Morse 1985). These spiders were removed from their natural nest sites within a week of laying and placed on a variety of sites for 1-hour periods, and their movements recorded during this time. Spiders were characterized as active if they moved on the nest or changed orientation five or more times per hour, or if they left the nest during this time. A random sample of spiders brooding their own eggs moved 3.3 ± 3.8 times per h ($\bar{x} \pm SD$) ($N = 34$) (Morse 1987).

Tests included spiders removed from and then returned to their own nests and ones placed on other *M. vatia* nests; as well as individuals placed on superficially similar nests of other thomisid, salticid, and theridiid spiders; on unaltered milkweed leaves; on leaves turned under by spiders or by the investigator; and on leaves with *M. vatia* nest silk placed on them. Controls were also run to determine that one-hour periods insured a representative bout of behavior. After the experiments the spiders were returned to their own nest sites. For comparison, similar transplantation experiments were run on two other groups of spiders: "broody" spiders, which had turned under leaves preliminary to egg-laying; and large, actively-feeding spiders. Both were placed on completed *Misumena* nests. All of these presentations were sequential, in keeping with the natural patterns observed in the field. Thirty spiders were used in each experiment, none of the individuals in more than one experiment.

Another group of spiders was periodically tested for recognition of their own nests over the entire period that they normally would guard nests. I removed these individuals from their nests immediately after they laid their eggs and

Table 1.—Responses and activity levels of spiders placed on different substrates. Only the first 15-16 replicates were scores for activity in Experiments 2-11. $N = 30$ in each experiment. a = All at guarding stage except for Experiments 10 and 11. b = Had turned under leaf preparatory to laying. Laid 1-5 days later ($\bar{x} \pm SD = 2.5 \pm 0.7$ days). c = Actively hunting and showing no indication of nest building. Laid 4-12 days later ($\bar{x} \pm SD = 8.2 \pm 3.9$ days).

Experiment	Treatment ^a	Remain on site	Leave site	Stationary	Active
1	Monitor, remove & return				
	Before removal	30	0	25	5
	After return	30	0	22	8
2	On other nest and return				
	On other nest	29	1	12	18
	After return	30	0	20	10
3	Unaltered leaf	4	26	1	14
4	Leaf turned under by spider	14	16	4	11
5	Nest silk on leaf	15	15	6	9
6	Artificial nest	19	11	8	7
7	<i>Xysticus</i> nest	18	12	4	11
8	<i>Metaphidippus</i> nest	15	15	7	8
9	<i>Enoplognatha</i> nest	10	20	4	11
10	<i>Misumena</i> nest ^b	13	17	8	7
11	<i>Misumena</i> nest ^c	5	25	3	13

completed their nests. They were placed inside large bags of nylon tricot that covered plants similar to the ones upon which they laid and subsequently kept in these bags, except when they were run in experiments on their own nests, either once or every several days. These manipulations permitted an assessment of whether time away from the nest affected the tendency to guard a nest.

RESULTS

Experiment 1. Spiders removed from their own nest and returned.—In an initial test, several spiders were monitored for an hour to record activity, then removed from their nests, moved about their home milkweed clone in a small shell vial concealed from any possible visual cues, and returned to their sites and monitored for another hour. Only a small percentage of the individuals exhibited regular activity prior to removal (Table 1), and this number did not differ significantly from those exhibiting activity after their return ($G = 0.89$, $P > 0.3$). Thus, removal in itself does not measurably affect the behavior of these species and should not be the basis for any differences reported in Experiments 2-9 presented below. This pattern of low activity characterizes guarding spiders (see Methods).

Experiment 2. Spiders switched to other recently-occupied *Misumena vatia* nests.—Spiders laying at similar times were removed from their nests and immediately placed on each others' nests for an hour. During this period one of the 30 individuals left the nest after 5 min. It was replaced and remained the next 55 min until removed. All other individuals remained on their foster nests for the full 1-hour period. Thus, no significant difference occurred between the tendency to remain on their own nests (Experiment 1) and those of other individuals at a similar stage of development ($G = 1.40$, $df = 1$, $P > 0.2$). However, the activity

of these displaced spiders on different nests was greater than that of similarly displaced ones returned to their own nests (Experiment 1) ($G = 6.93$, $P < 0.01$). The spiders made several lines that secured the nest to nearby leaves or other structures. The spiders became less active when they were returned to their own nests after one hour, ($G = 4.34$, $P < 0.05$) (Table 1), but some activity still remained. The number of active individuals did not significantly exceed that of Experiment 1 ($G = 0.16$, $P > 0.5$).

Experiment 3. Bare milkweed leaves.—I placed spiders on leaves of similar size and location to those used for nests, which had not been manipulated by spiders. Only four of the 30 *M. vatia* placed on these leaves remained for an hour, which differs significantly from the behavior of spiders returned to their own nests ($G = 58.55$, $P < 0.001$) or put on other *M. vatia* nests ($G = 50.25$, $P < 0.001$). Clearly spiders do not respond to unmodified leaves in the way that they respond to their own nests or those of conspecifics. This experiment indicates that the spiders are active enough to leave their sites within an hour. Failure of the spiders in Experiments 1 and 2 to move from the nests is thus not a consequence of a low rate of activity.

Experiment 4. Leaves with tips turned under by other *Misumena vatia*.—One of the distinctive features of a *M. vatia* nest is that the leaf used is turned down at the tip and folded under by the parent spider (Morse 1985: fig. 1). The first step in making a nest is to turn a leaf under and secure it with strands of silk between the distal tip and the ventral side of the leaf's midrib. After performing this act spiders typically remain in the resulting shelter for 1-3 days before laying their eggs and drawing the sides of the leaf tightly together with silk to complete the nest. This position differs from the one assumed by spiders that have already laid their eggs. Several spiders were collected for experiments at the leaf-turning stage, resulting in a ready source of such leaves for this experiment. Only 14 of 30 brooding spiders placed on these leaves remained there for the full test period. This response is significantly weaker than from the response to both their own nests ($G = 78.13$, $P < 0.001$) (Experiment 1) and to the nests of other *M. vatia* ($G = 21.30$, $P < 0.001$) (Experiment 2), but significantly stronger than the response to unmodified leaves (Experiment 3) ($G = 8.29$, $P < 0.01$). Thus, turned-under leaves appear to be a stimulus for remaining at a site, although not as strong a stimulus as a completed nest.

Experiment 5. Leaves with *Misumena vatia* silk applied to their distal ends.—Another potentially important feature promoting site tenacity might be the presence of silk. *Misumena vatia* place considerable amounts of silk about their nests, noticeably stiffening the distal part of the leaf. This silk can be readily removed as a sheet from the surface of the nests. In Experiment 5, sheet-like silk was removed from other nests and placed on the distal 1 cm of both upper and lower surfaces of otherwise undisturbed leaves similar to those usually used as nest sites. Except for the silk added, these leaves were similar to the leaves used in Experiment 3.

Half of the spiders remained on these sites during the experiment. Their frequency of staying is significantly lower than that of spiders placed on the nests of other conspecifics ($G = 19.23$, $P < 0.001$) (Experiment 2) or returned to their own nests ($G = 25.89$, $P < 0.001$) (Experiment 1). This response was stronger than the response to plain leaves (Experiment 3) ($G = 9.77$, $P < 0.01$) but not the response to turned-under leaves (Experiment 4) ($G = 0.07$, $P > 0.7$). Thus, the

presence of silk also appears to play a role in determining what constitutes a nest, but it is not as strong as a completed nest.

Experiment 6. Artificial nests secured by thread.—It is possible that the results in Experiment 4 were a consequence of the distal and medial parts of the leaves being only partly apposed to themselves, rather than due to a lack of silk. To test this possibility, I sewed leaves into the form of nests with fine white thread, placing segments of dried timothy grass (*Phleum pratense* L.) inflorescences inside to approximate the shape of a nest. Spiders in this experiment could not crawl inside the nest, which distinguishes this manipulation from Experiment 4.

A majority of the spiders remained on these artificial nests for the entire period of the experiments. This result did not differ from that of Experiment 4 (leaves turned under by spiders), in which the spiders had access to leaves partially turned under by spiders ($G = 1.69$, $P > 0.1$). It was weaker than the response to the nests of other *M. vatia* (Experiments 1 and 2), however ($G = 17.74$ and 11.85 , $P < 0.001$, < 0.001). Thus, turned-under, closed leaves may provide important cues for spiders, but further experiments would be required to establish whether they differ from simple turned-under leaves.

Experiment 7. Nests of other species of crab spiders—*Xysticus emertoni*.—The brown crab spider *Xysticus emertoni* (Keyserling) sometimes places its egg sacs in positions similar to those of *M. vatia*. *Misumena vatia* placed on *X. emertoni* nests remained significantly more frequently than they did on unaltered milkweed leaves (Experiments 1 and 2) ($G = 19.67$, 14.97 , $P < 0.001$, < 0.001). However, their response did not differ from those to turned-under leaves ($G = 1.07$, $P > 0.2$), silked leaves (Experiment 5) ($G = 0.61$, $P > 0.3$) or artificial nests (Experiment 6) ($G = 0.07$, $P > 0.7$).

Experiment 8. Jumping spider nests.—The small jumping spider *Metaphidippus insignis* (Banks), abundant in the study area, builds nests on milkweed leaves that are similar in location and general characteristics to *M. vatia* nests and guarded from within. Half of the *M. vatia* placed on *M. insignis* nests remained on them for the entire hour. Thus they responded more strongly to them than they do to bare leaves (Experiment 3) ($G = 9.77$, $P < 0.01$) and more weakly than to their own nests (Experiment 1) ($G = 25.89$, $P < 0.001$). However, their response does not differ significantly from the response to the artificial nests (Experiment 6) ($G = 1.09$, $P > 0.2$).

Experiment 9. Theridiid spider nests.—A theridiid spider *Enoplognatha ovata* (Clerck) occurs in the study area in small numbers. It also builds nests by turning under leaves (Wise and Reillo 1985), often milkweed leaves, but these nests are less stiff than *M. vatia* nests, probably because *Enoplognatha ovata* do not use large amounts of sheet-like silk in construction. They also guard their nests from inside. Nests built on milkweed leaves were chosen for a set of experiments.

Only one-third of the *M. vatia* remained on *E. ovata* nests for an hour, significantly fewer than the number that remained on their own nests (Experiment 1) ($G = 38.19$, $P < 0.001$), or artificial nests (Experiment 6) ($G = 5.49$, $P < 0.02$). However, this result does not differ significantly from the number remaining on plain leaves (Experiment 3) ($G = 3.44$, $P > 0.1$) or *M. insignis* nests ($G = 1.72$, $P > 0.1$).

Experiment 10. Pre-laying *Misumena vatia* placed on nests.—Spiders that had already turned under leaves in apparent preparation for egg laying ("broody") were placed on completed nests, as in Experiment 2. Significantly fewer

individuals remained on the nests for an hour than did post-laying individuals on other nests (Experiments 1 and 2) ($G = 30.47$ and 23.48 , $P < 0.001$, < 0.001). Although relatively active at this time, spiders did exhibit a significantly greater tendency for site tenacity prior to laying their own eggs than did post-laying individuals on a plain leaf (Experiment 3) ($G = 6.91$, $P < 0.01$).

Experiment 11. Active *Misumena vatia* placed on nests.—A group of spiders within the size range of egg-laying individuals, but which had not shown any signs of broodiness (i.e., ones that had not turned under a leaf, and were still actively hunting), were also tested. These spiders showed relatively little tendency to remain on nests, significantly fewer remaining than for the broody group (Experiment 10) ($G = 5.22$, $P < 0.05$), or individuals that had already laid (Experiments 1 and 2) ($G = 54.47$ and 46.31 , $P < 0.001$, < 0.001). These individuals did not differ from post-laying spiders that were placed on leaves randomly (Experiment 3) ($G = 0.13$, $P > 0.5$).

Experiment 12. The effect of time away from nest on response.—Individuals in Experiments 1-11 were tested within a few days of laying their eggs. The tendency to remain could thus be a consequence of whether a spider was already guarding its nest. If spiders maintain strong site tenacity, contact with the nest might suffice to retain a predisposition to guard. However, if somehow separated from its nest, the spider might sometimes reoccupy it in the process of random movement by contacting the lines of silk in the vicinity of the nest that are normally laid wherever an individual goes. In the process of this study two spiders, both of known history, that had earlier left their nests established residence at abandoned nests of other conspecifics. These observations are consistent with individuals becoming separated from their own nests, but retaining an affinity to nest cues. These two individuals had been away from their own nests only one and three days, however, which raised the question of how long they would retain this predisposition in the absence of regular contact with nests.

Spiders removed from their nests after laying and placed in nylon tricot bags on similar plants exhibited a strong correlation between time of separation from the nest and tendency to guard when returned (Fig. 1). This ranged from an 88% tendency to remain when away from the nest for 1-5 days to a 20% tendency to remain when removed from 26-30 days, roughly the period between laying and emergence of young (Morse 1987). The pattern of decrease in tendency to remain appears to be somewhat stepped, but relatively slow. The number of confined individuals remaining on their former nest sites for the 1-hour testing period was significantly lower than that of unconfined, free-living individuals at each period ($G = 4.40$, $P < 0.05$ for one five-day period to $G = 9.82$, $P < 0.01$ for the 6-10 day period), suggesting that absence from the nests affects the probability of remaining on them.

This test measures the effect of absence from the nest; however, since each period away from the nest was about 5 days, it does not directly measure true time away from nests. Each of these individual tests might represent a mere five-day absence to the spider, whether five or 30 days from the initial removal. Individuals away from the nests 15 and 30 days from the initial removal were used to compare these effects (Fig. 1). They revealed no clear difference, falling very close to the periodic removals at 11-15 days ($G = 0.03$, $P > 0.8$) and not

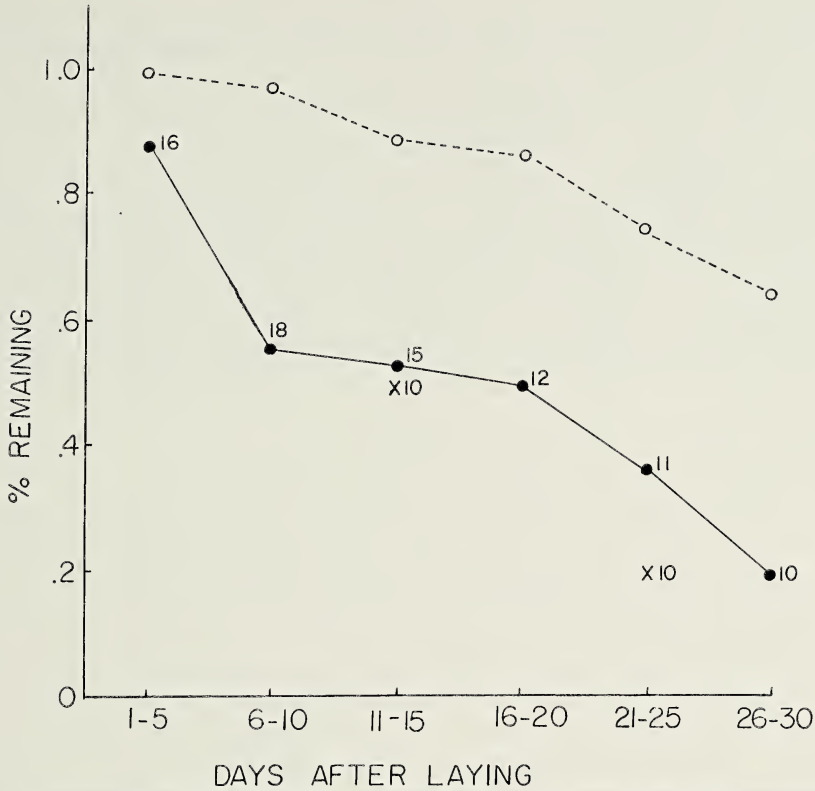


Figure 1.—Percentage of spiders remaining on their nests for one hour after being separated from these nests for five-day intervals (filled circles), percentage remaining for one hour if separated for 11-15 or 21-25 days (x's). Numbers to right of symbols are *N*'s. Percentage of 37 unscreened nesting individuals remaining on nest at the same time in the study area (open circles).

significantly different at 21-25 days, at a time that the tendency to remain at the nest was dropping rapidly ($G = 0.70$, $P > 0.3$).

Experiment 13. Tenure times of natural and cross-fostered spiders.—The cross-fostered individuals remained on their new nests for a period similar to that of undisturbed spiders ($\bar{x} \pm SD = 29.3 \pm 11.7$ vs 27.6 ± 13.3 days, $N = 40, 30$; $P > 0.5$ in a two-tailed Mann-Whitney *U*-Test). This result further supports the conclusions from Experiment 2. Thus, both Experiments 1 and 2 are probably typical of the results that would be obtained if they were to be run for more than one hour.

DISCUSSION

The response of *Misumena vatia* to these stimuli does not appear to be individual-specific, or even species-specific. It appears related to shape and tactile characteristics. The difference in activity between spiders returned to their own nest or placed on a conspecific's nest appeared to be related to the presence or absence of silken lines to adjacent leaves. Active individuals spent much of their time spinning these lines. The response of the spiders to a variety of different stimuli suggests that multiple factors play a role in nest retention. Leaves turned under by other spiders, leaves with spider nest silk affixed to them, and

artificially constructed nests (Experiments 4-6) all elicited a much more frequent response than did unaltered leaves (Experiment 3), although not as strong a response as to complete nests (Experiments 1 and 2). Resemblance of other spiders' nests to one or both cues was probably the key factor in determining how *M. vatia* responded to them (Experiments 7-9). The frequency of the response could be a consequence of either the characteristics of the silk, or of its volume. *Enoplognatha ovata* nests are extremely pliable in comparison to the other nests, especially the *M. vatia* nests, probably because members of this species apply less silk to the outside of their nests than do the others. If *M. vatia* respond primarily to tactile cues, they might perceive *E. ovata* nests as quite different from their own. Alternatively, the spiders may have responded primarily to the shape of the nests. This explanation is supported by their relatively strong response to the artificial nests.

Does the ability to reclaim a lost nest site have any selective significance, given that individuals normally occupy their nests continually, so that site tenacity itself might normally suffice to insure continuous occupation? Several factors may result in short-term disappearance, and, with the advantage that guarded nests produce more offspring than unguarded ones (Morse in press), reoccupation should be favored. I have observed several instances of temporary disappearance of *M. vatia* females from their nests in response to potential predators of either the spider or the egg mass. In 1983, several egg masses were attacked by an unknown predator. Two females that disappeared from their nest plants at this time returned to their nests within a day and resealed them tightly with silk. Spiderlings subsequently emerged from remaining uneaten eggs in both nests. Another spider was driven from its nest by ants (*Formica* sp.) shortly after completing it. It left the plant at this time, but reoccupied its nest within a day. Deer (*Odocoileus virginianus*) occasionally feed on milkweed in small amounts (Wilbur 1976), and I have had one spider nest inadvertently consumed in this way. Another nest plant was badly damaged at the same time, and the spider disappeared in the process. However, it reappeared the following day and secured its badly damaged nest in a way that protected it through the rest of the nesting period.

Individuals that have left their nests occasionally occupy other individuals' nests, thereby confirming the experimental results demonstrating that site tenacity was not confined to individuals' own nests. I have recorded two instances in which marked individuals have occupied nests earlier abandoned by other individuals. I also have one record of a displaced *M. vatia* occupying a *X. emertoni* nest.

These observations support the experiments, suggesting that displaced spiders sometimes find their way back to their nests, but that any such ability results from a general response that may produce an inappropriate relocation. Since the spiders are usually sedentary at this time and do not nest at high densities, most reoccupations are likely to occur on their own nest.

The decrease in acceptance of nests over time by the bagged individuals closely matched the disappearance of undisturbed spiders from their nests (Morse 1987). This result suggests that the removed individuals' behavioral patterns are relevant to those of undisturbed guarding spiders. The similarity in responses of individuals periodically returned to their nests and those only returned a single

time suggests that the tendency to reoccupy a nest is not related to time away from a nest, but to the actual condition of the spider.

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TWO NEW SPECIES OF KLEPTOPARASITIC *MYSMENOPSIS* (ARANEAE, MYSMENIDAE) FROM JAMAICA

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ABSTRACT

Two new species of kleptoparasitic *Mysmenopsis* spiders (*M. monticola* and *M. furtiva*) from Jamaica are described; diagnoses and natural history data are also provided. These sister species appear to have coevolved with their respective host populations of *Ischnothele*, also each other's closest relatives. The probable close relationship of this *Mysmenopsis* species pair to *M. tibialis* (Bryant) is discussed.

INTRODUCTION

As defined by Platnick and Shadab (1978), *Mysmenopsis* includes 18 known species of tiny tropical and subtropical American mysmenid spiders with cusps attached distally to the male palpal tibia. These spiders are of special interest because at least some of them live as kleptoparasites (food stealers) in the funnelwebs of diplurid spiders (Platnick and Shadab 1978; Vollrath 1978). In this paper we describe two new *Mysmenopsis* species, which the first author, in the course of research on the systematics of ischnotheline diplurids, recently discovered living in *Ischnothele* webs in Jamaica. We also discuss the relationships of these new species and include observations on their natural history.

RELATIONSHIPS

The large number of character states shared by these two Jamaican *Mysmenopsis* species, including many similarities in male and female genital characters, clearly indicates that these are sister species. Several female character states, in particular, are probably synapomorphic for these two species: 1) a pair of spherical spermathecal chambers on each side of the epigynum (Figs. 16, 31), 2) comma-shaped posterior spermathecal lobes (Figs. 16, 31), 3) epigynal apex somewhat keel-shaped dorsally (Figs. 16, 31), 4) a rough retrolateral protuberance at distal end of femur I (Figs. 11, 27, 28), and 5) the absence of spines on metatarsus I. It is important to point out that each of these species was found living with a different member of a pair of undescribed allopatric *Ischnothele* morphs which also appear to be sister species (differing in color, habitat, and very few morphological traits) (Coyle in preparation). This appears to be the first clear

evidence for the kind of host-symbiont cospeciation process which Platnick and Shadab (1978) suggested might play a role in *Mysmenopsis* evolution.

Of all the previously described species of *Mysmenopsis*, *M. tibialis* (Bryant) is most similar to, and consequently seems most closely related to, these Jamaican species; however we should point out that our failure to examine specimens of any *Mysmenopsis* species other than *M. tibialis* [we relied upon Müller (1987), Platnick and Shadab (1978), and earlier descriptions] and the fact that males of some *Mysmenopsis* species are unknown make this hypothesis especially tentative. The following character states appear to be synapomorphies uniting the Jamaican species and *M. tibialis* [the unknown males of *M. wygodzinskyi* and *M. schlingeri*, which in Platnick and Shadab's (1978) cladogram form a trichotomy with *M. tibialis*, may be found to share some of these apomorphies]: 1) epigynum on end of pleated lobe (Figs. 5, 6, 17, 18, 32, 33), 2) embolar base sharply delimited from bulb (Figs. 9, 25), 3) male palpal patella with distal retrolateral keel (Figs. 9, 10, 25, 26), 4) sperm duct of palpal organ with a distinctive pattern of loops (Figs. 9, 25), and 5) cusps on male palpal tibia greatly reduced or lost.

The examination of *M. tibialis* types revealed that the palpal sperm duct is looped as in the Jamaican species (Figs. 9, 25), not as shown in Platnick and Shadab's (1978) fig. 59 of a paratype palp. Also, we could not see (using the dissecting microscope at 100 and 200X magnification) the small cusps illustrated by Platnick and Shadab (1978, fig. 59) on the inside of the tibial ledge. We suggest that the absence of tibial cusps in the Jamaican species is not plesiomorphic but the result of a secondary loss, and that the very small cusps of *M. tibialis* (if present) represent a stage in that loss process. We have redrawn the epigynum of *M. tibialis* (Figs. 5-7) to reveal more clearly than in the illustrations of Bryant (1940) and Platnick and Shadab (1978) some of the character states which suggest a close relationship to the Jamaican species.

Our hypothesis that *M. tibialis* is the sister species of the two Jamaican species is in conflict with synapomorphies 6 and 7 in Platnick and Shadab's (1978) cladogram. If their interpretation of those two character states is valid and if our hypothesis is correct, it is necessary to postulate that the anterior spermathecal ducts and female metatarsus I spines were reduced or lost in the ancestor of the Jamaican species.

Platnick and Shadab (1978) suggested that *M. palpalis*, which they placed in a clade with *M. tibialis* and two other species, may be misplaced and belong instead to a clade of six species which includes *M. cidrelicola*, because, of the five *Mysmenopsis* species known to be kleptoparasites, *M. palpalis* was the only one not in the *M. cidrelicola* clade. Given the evidence that the two new kleptoparasitic species are probably members of the *M. tibialis* clade, it is no longer necessary to suggest on the basis of kleptoparasitic habits that *M. palpalis* is misplaced (although it may eventually prove to be misplaced on the basis of other characters). Based upon the kleptoparasitic nature of the Jamaican species, we predict that *M. tibialis*, and perhaps *M. schlingeri* and *M. wygodzinskyi*, will prove to be kleptoparasites.

METHODS

The quantitative characters used in this study are abbreviated and defined as follows: BL, total body length; CL, carapace length; CW, carapace width; SL, sternum length; SW, sternum width; IFL, ITL, IML, and ITarL, lengths of leg I

articles; ITX, distance along longitudinal axis of male tibia I from perpendicular line through distal edge of tibial spur tubercle base to perpendicular line through proximal point of articulation; IFT, maximum diameter of male femur I; ITT, diameter of male tibia I at distal edge of tibial spur tubercle base; ITS, distance from tip of male tibial spur to distal edge of its tubercle base; PTW, maximum width of male palpal tibia perpendicular to longitudinal axis of cymbium; EBW, maximum width of embolus base; DTA, distance along longitudinal axis of female femur I from perpendicular line through ventral tubercle apex to proximal end of femur; FDT, maximum diameter of female femur I including ventral tubercle; HFT, height of female femur I tubercle (distance from tubercle tip to point of most abrupt slope change at junction of tubercle and edge of femur); EL, distance from posterior (distal) tip of epigynum to anterior edge of spermatheca chamber (Fig. 33); EPL, distance from anterior edge of spermatheca chamber to junction of dorsoposterior surface of epigynum with ventral surface of abdomen (Fig. 33); EW, width of epigynum at anterior (proximal) end of sclerotized plate (Fig. 17).

BL was measured in side view. All carapace and sternum measurements were performed from a ventral view with the lateral borders of the sternum in the horizontal plane. CW endpoints were at the intersections of the carapace edge and the retrolateral surface of legs II. The length of each leg I article was measured in retrolateral view and equals the distance from the proximal point of articulation to the most distal point of the article. IFT and PTW were measured from a retrolateral view. ITX was measured from an approximately retrolateral view with the tibial spur in the horizontal plane. ITT and ITS were measured from an approximately prolateral view with the tibial spur in the horizontal plane. DTA, FDT, and HFT were measured from a view between ventral and retrolateral with the ventral tubercle in the horizontal plane so that the HFT value was the maximum possible. IFT, ITT, FDT, and HFT were measured perpendicular to the longitudinal axes of their respective articles. EL and EPL were measured from a side view (left) of the abdomen; EW was measured from an approximately ventral view with the epigynum in the horizontal plane. All appendage measurements were recorded from the left appendage, unless it was damaged, missing, or not fully regenerated (in which case the right appendage was measured).

Measurements were performed with a Wild M-5 stereomicroscope with 20X ocular lenses and an eyepiece micrometer scale. BL measurements were performed at 50X and are accurate to 0.018 mm, and all other measurements were performed at 100X and are accurate to 0.009 mm. All measurements are given in millimeters.

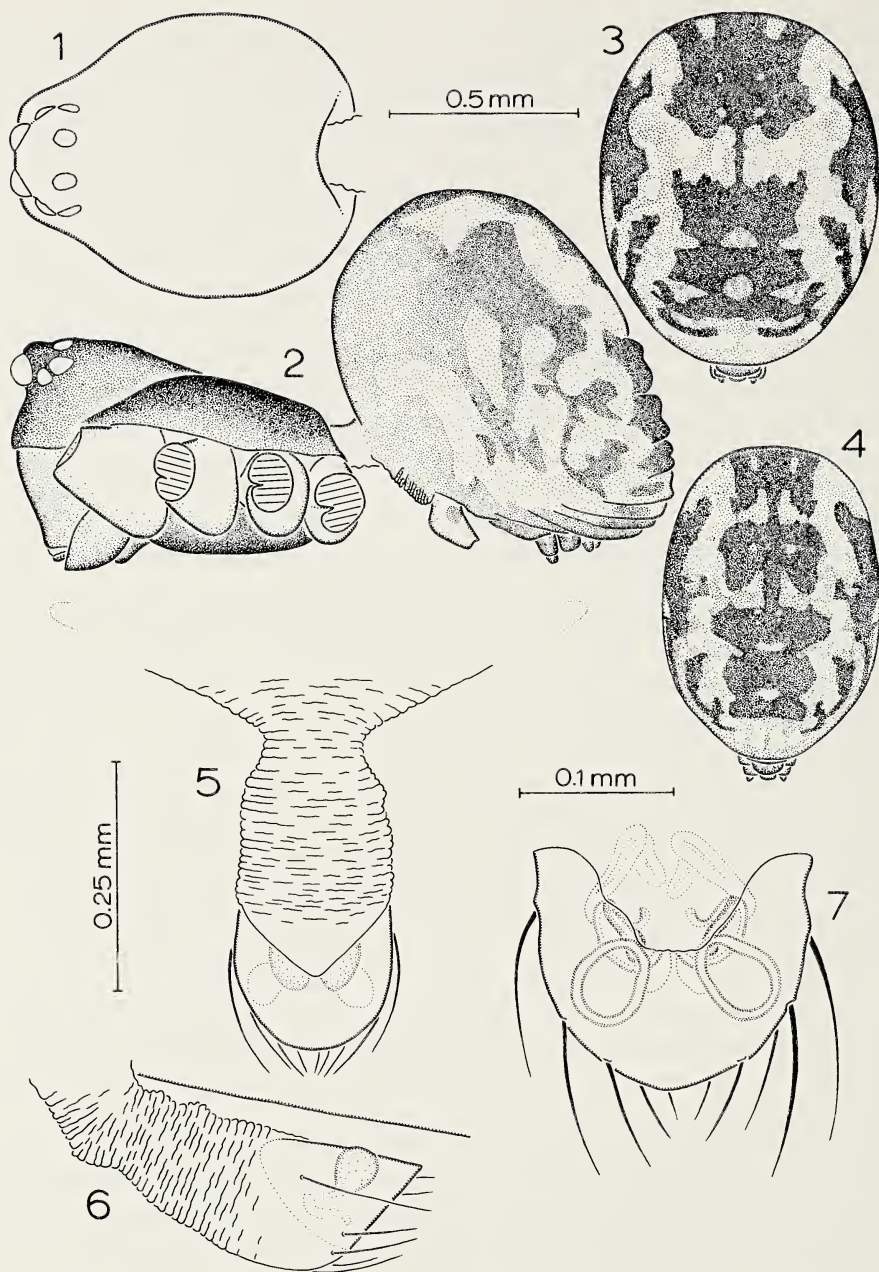
Spermathecae were cleared in 85 percent lactic acid, viewed at 400X through a compound light microscope, and drawn with the aid of a drawing tube.

Each species description is a composite of all the adult specimens examined; these sample sizes are given in Tables 1 and 2. The quantitative character values recorded in these tables are an integral part of each description.

Mysmenopsis monticola, new species

Figs. 1-3, 8-23, 39-42

Types.—Male holotype and six male and 13 female paratypes collected in *Ischnothele* webs on roadbanks in humid mountain forest along road between



Figures 1-7.—*Mysmenopsis* spp.: 1-3, *M. monticola* paratypes; 1, female carapace, dorsal; 2, female body, lateral; 3, male abdomen, dorsal; 4, *M. furtiva* paratype male abdomen, dorsal; 5-7, *M. tibialis* paratype epigynum; 5, ventral; 6, lateral; 7, cleared, dorsal. Scale lines: 0.5 for Figs. 1-4; 0.25 for Figs. 5, 6; 0.1 for Fig. 7.

Newcastle (3800 ft elevation) and Hardwar Gap (4200 ft elevation), St. Andrews Parish, Jamaica (8 April 1988; F. Coyle, R. Bennett, and A. Robinson), deposited in the American Museum of Natural History.

Etymology.—The specific name refers to the montane habitat of this species.

Diagnosis.—Males of *M. monticola* can be distinguished from those of *M. furtiva* by the following differences: 1) The embolus base is wider (Fig. 9) [EBW

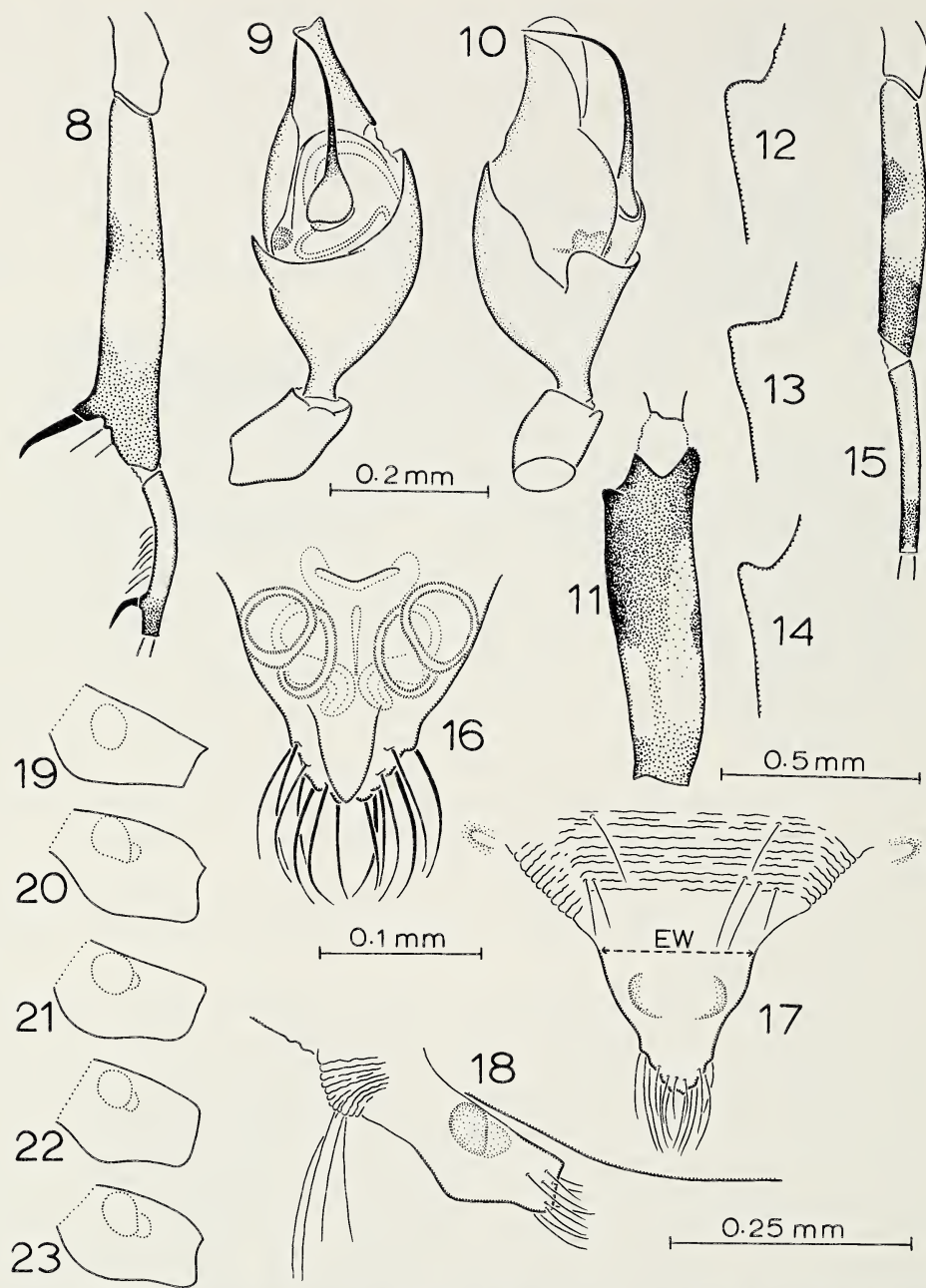
= 0.056; $EBW(100)/PTW = 25-30, 26.8 \pm 1.60$] than in *M. furtiva* (Fig. 25) [$EBW = 0.037$; $EBW(100)/PTW = 22-24, 22.7$]. 2) The embolus tapers more abruptly above its base in retrolateral view (Fig. 9) and is more evenly curved in ventral view (Fig. 10) than in *M. furtiva* (Figs. 25, 26). 3) The ventral ledge on the palpal tibia forms a proportionally larger lobe (Figs. 9, 10) than in *M. furtiva* (Figs. 25, 26). 4) The tibia I clasping spur (including the tubercle from which it arises) is longer (Figs. 8, 41) [$ITS = 0.194-0.241, 0.213 \pm 0.015$; $ITS(100)/ITT = 169-192, 180.9 \pm 7.59$] and more distal [$ITX(100)/ITL = 84-89, 85.8 \pm 1.59$] than in *M. furtiva* (Figs. 24, 41) [$ITS = 0.157-0.176, 0.167$; $ITS(100)/ITT = 150-158, 154.3$; $ITX(100)/ITL = 80-83, 81.0$].

Females of *M. monticola* can be distinguished from those of *M. furtiva* by the following differences: 1) The femur I ventral tubercle (Figs. 11-14, 39, 40) is larger [$HFT = 0.046-0.083, 0.055 \pm 0.012$; $HFT(100)/IFL = 5.1-8.0, 6.38 \pm 1.00$], its proximal slope is much less steep, and it is more prolateral and distal [$DTA(100)/IFL = 84-90, 86.8 \pm 1.61$] than in *M. furtiva* (Figs. 27-30, 39, 40) [$HFT = 0.019-0.037, 0.026 \pm 0.009$; $HFT(100)/IFL = 2.7-4.4, 3.42 \pm 0.75$; $DTA(100)/IFL = 75-77, 75.9 \pm 0.81$]. 2) The rough swelling on the retrolateral side of the distal end of femur I (Fig. 11) is much less prominent than the homologous tubercle (Figs. 27, 28) in *M. furtiva*. 3) The epigynum is at the end of a pleated lobe which is usually broader and shorter (Figs. 17, 18) ($EPL = 0.009-0.074, 0.031 \pm 0.023$) than in *M. furtiva* (Figs. 32, 33) ($EPL = 0.065-0.278, 0.176 \pm 0.071$). 4) The epigynum has a pronounced distoventral expansion (Figs. 18-23) which is lacking in *M. furtiva* (Figs. 33-38). 5) The epigynal hairs extend beyond the end of the epigynum more than one-third of the length of the epigynum (Figs. 16-18) instead of much less than one-third the epigynal length (Figs. 31-33). 6) The lip of the epigynal opening is broad and well-sclerotized (Fig. 16), not U-shaped and very weakly sclerotized as in *M. furtiva* (Fig. 31).

Both sexes of *M. monticola* exhibit on the abdominal dorsum (Fig. 3) a light grey H-shaped pigment pattern that is different from the pattern of *M. furtiva* (Fig. 4) (see description).

The following characters best separate *M. monticola* and *M. furtiva* from their close relative, the Cuban species, *M. tibialis*, (see Platnick and Shadab 1978, figs. 59-64): 1) No apophysis arises from the embolus base (Figs. 9, 25) as in *M. tibialis*. 2) The ventral lobe-like ledge on the male palpal tibia (Figs. 9, 10, 25, 26) is not present in *M. tibialis*. 3) The male palpal patellar keel is broader, thinner, and sharper (Figs. 9, 25) than in *M. tibialis*. 4) The male tibia I spur is more sharply bent near its distal end and its tubercle is shorter (Figs. 8, 24) than in *M. tibialis*. 5) Female tibia I (Fig. 15) lacks the ventral tubercle and female metatarsus I (Fig. 15) lacks the spine row present in *M. tibialis*. 6) The female femur I ventral tubercle and distal retrolateral protuberance (Figs. 11, 27) are not present in *M. tibialis*. 7) Several differences exist in the form of the epigynum and spermathecae (Figs. 5-7, 16-18, 31-33).

Males.—Table 1. Figs. 3, 8-10, 41. Palpal patella with sharp distal keel on retrolateral surface. Palpal tibia with ventral ledge produced into rather large lobe; no cusps associated with this ledge. Embolus with relatively broad base; narrows abruptly above base; smoothly curved in S-shape, ending at distal edge of cymbium. Tibia I clasping spur attached to moderately short tubercle and bent distally. Legs with dark patches on pale tan background; coxae mostly unpigmented; femur I mostly dark, rest of femora with dark spot in middle and



Figures 8-23.—*Mysmenopsis monticola*: 8-10, holotype male; 8, tibia and metatarsus I, approx. prolateral; 9, 10, palp; 9, retrolateral; 10, ventral; 11-23, paratype females; 11, femur I, ventral; 12-14, femur I ventral tubercle of three specimens, view between ventral and retrolateral; 15, tibia and metatarsus I, prolateral; 16-23, epigyna; 16, cleared, dorsal; 17, ventral; 18-23, lateral view of six specimens. Scale lines: 0.2 for Figs. 9, 10, 12-14; 0.5 for Figs. 8, 11, 15; 0.1 for Fig. 16; 0.25 for Figs. 17-23.

at both ends; patellae with dark spot; tibiae with dark spot in middle and distally; metatarsi with distal dark spot; tarsi unpigmented. Carapace and sternum dark grey. Abdomen with many areas of dark grey or black separated by areas of light

Table I.—Quantitative character values for *Mysmenopsis* males. Character abbreviations are defined in the methods section of the text. All measurements given in millimeters. Range, mean, and standard deviation given for samples larger than four.

	<i>monticola</i> (N=7)	<i>furtiva</i> (N=3)	<i>monticola</i> holotype	<i>furtiva</i> holotype
BL	1.39-1.72 (1.53±0.12)	1.33-1.55 (1.43)	1.61	1.41
CL	0.71-0.81 (0.748±0.038)	0.66-0.73 (0.688)	0.79	0.68
CW	0.59-0.70 (0.643±0.041)	0.56-0.62 (0.586)	0.68	0.58
SL	0.46-0.53 (0.486±0.029)	0.43-0.46 (0.441)	0.52	0.43
SW	0.44-0.51 (0.468±0.029)	0.42-0.45 (0.432)	0.51	0.43
IFL	0.81-1.06 (0.926±0.087)	0.76-0.84 (0.799)	1.06	0.80
ITL	0.69-0.88 (0.766±0.070)	0.64-0.70 (0.666)	0.88	0.66
IML	0.38-0.44 (0.404±0.021)	0.33-0.35 (0.342)	0.43	0.33
ITarL	0.42-0.45 (0.432±0.015)	0.34-0.35 (0.348)	0.45	0.34
ITX	0.57-0.75 (0.658±0.063)	0.51-0.56 (0.540)	0.75	0.55
IFT	0.185-0.305 (0.251±0.041)	0.222-0.259 (0.237)	0.296	0.231
ITT	0.111-0.129 (0.118±0.007)	0.102-0.111 (0.108)	0.130	0.111
ITS	0.194-0.241 (0.213±0.015)	0.157-0.176 (0.167)	0.241	0.167
PTW	0.185-0.222 (0.207±0.012)	0.157-0.167 (0.163)	0.213	0.167
EBW	0.056 (0.056±0.0)	0.037 (0.037)	0.055	0.037
ITX(100)/ITL	84-89 (85.8±1.5)	80-83 (81.0)	85	83
ITS(100)/ITT	169-192 (180.9±7.5)	150-158 (154.3)	186	150
EBW(100)/PTW	25-30 (26.8±1.6)	22-24 (22.7)	26	22

grey with white spots; dorsally, two prominent, longitudinal, winding light grey bands separated by dark central area except for one pair of broad median lobes of light grey that almost connect at median line to produce light grey "H" pattern.

Females.—Table 2. Figs. 1, 2, 11-23, 39, 40. Femur I with prominent tubercle on prolateral aspect of ventral surface near distal end; tubercle with gently sloping proximal face, steep distal face, and rounded apex; rough-surfaced retrolateral swelling at distal end of femur. Tibia I cylindrical. Metatarsus I without spines. Epigynum at end of short, broad, unsclerotized, pleated lobe; tip with rough rounded distoventral prominence and rather sharp and keel-like distodorsal prominence; hairs extend well beyond tip; spermathecae consist of pair of oval chambers with curved posterior median lobe on each side, and broad, well-sclerotized lip bordering opening on ventral surface of epigynum. Pigmentation similar to that of males.

Variation.—We found relatively little variation in any of the characters in this population sample except for EPL (Table 2). The extremely wide range of epigynum lobe lengths may be due to pronounced developmental plasticity and/or use-induced changes during mating or oviposition. The pleated nature of the unsclerotized lobe suggests that it may be lengthened during these reproductive activities. Despite the wide range of EPL variation within both the *M. monticola* and *M. furtiva* samples, there is surprisingly little overlap between these samples. Variation in epigynum shape and femur I tubercle shape is illustrated by Figs. 18-23 and 12-14.

Natural history.—*Ischnothele* host webs were concentrated in or near humid forest on roadbanks ranging from low pebbly soil banks to tall rock outcrops and from heavily shaded and moist to more exposed and drier. The host population was quite dense; in two spots there were approximately 50 webs in a 6 m long by

Table 2.—Quantative character values for *Mysmenopsis* females. Character abbreviations are defined in the methods section of the text. All measurements given in millimeters. Range, mean, and standard deviation given.

	<i>monticola</i> (N=13)	<i>furtiva</i> (N=6)
BL	1.50-2.07 (1.67±0.13)	1.41-1.65 (1.51±0.08)
CL	0.73-0.87 (0.798±0.044)	0.65-0.79 (0.709±0.062)
CW	0.60-0.75 (0.660±0.048)	0.52-0.63 (0.569±0.047)
SL	0.47-0.57 (0.517±0.032)	0.41-0.50 (0.449±0.038)
SW	0.41-0.54 (0.467±0.039)	0.38-0.47 (0.419±0.037)
IFL	0.73-1.04 (0.867±0.090)	0.65-0.89 (0.749±0.100)
ITL	0.55-0.78 (0.645±0.068)	0.49-0.68 (0.567±0.079)
IML	0.41-0.55 (0.472±0.039)	0.37-0.47 (0.409±0.044)
ITarL	0.42-0.47 (0.438±0.017)	0.34-0.40 (0.367±0.026)
DTA	0.63-0.92 (0.754±0.084)	0.49-0.68 (0.569±0.077)
FDT	0.194-0.287 (0.236±0.030)	0.167-0.231 (0.197±0.031)
HFT	0.046-0.083 (0.055±0.012)	0.019-0.037 (0.026±0.009)
EL	0.102-0.139 (0.117±0.012)	0.093-0.129 (0.108±0.014)
EPL	0.009-0.074 (0.031±0.023)	0.065-0.278 (0.176±0.071)
EW	0.111-0.148 (0.133±0.011)	0.102-0.120 (0.109±0.007)
DTA(100)/IFL	84-90 (86.8±1.6)	75-77 (75.9±0.8)
HFT(100)/IFL	5.1-8.0 (6.38±1.00)	2.7-4.4 (3.42±0.75)

1.5 m tall section of roadbank. The retreat tubes penetrated into rock crevices, soil cavities, moss, and leaf litter. The retreats opened out onto exposed capture webs composed of one or two roughly horizontal sheets and other non-horizontal sheets and strands anchored to surrounding substrate and plant surfaces. The average capture web area was about 400 square cm, but the largest webs covered about 1000 square cm.

M. monticola were observed in many of the larger *Ischnothele* webs. Typically three to six mysmenids were seen per inhabited web, but as many as twelve were counted in one web. They were always observed in the capture portion of the host web near the retreat mouth. Adults of both sexes were found together in some of the host webs. Several females were carrying (it was not clear which appendages were being used) very thin-walled (nearly transparent) and roughly spherical egg sacs about equal to their body volume. Three of these egg sacs were collected and examined. One was 1.18 by 1.54 mm in size and contained nine eggs ranging in size from 0.41-0.46 mm minimum diameter to 0.51-0.55 mm maximum diameter. The other two egg sacs each contained four unpigmented pre-emergent spiderlings, but these sacs had been torn open (probably during or shortly after capture) and therefore may not have contained their full complement of spiderlings.

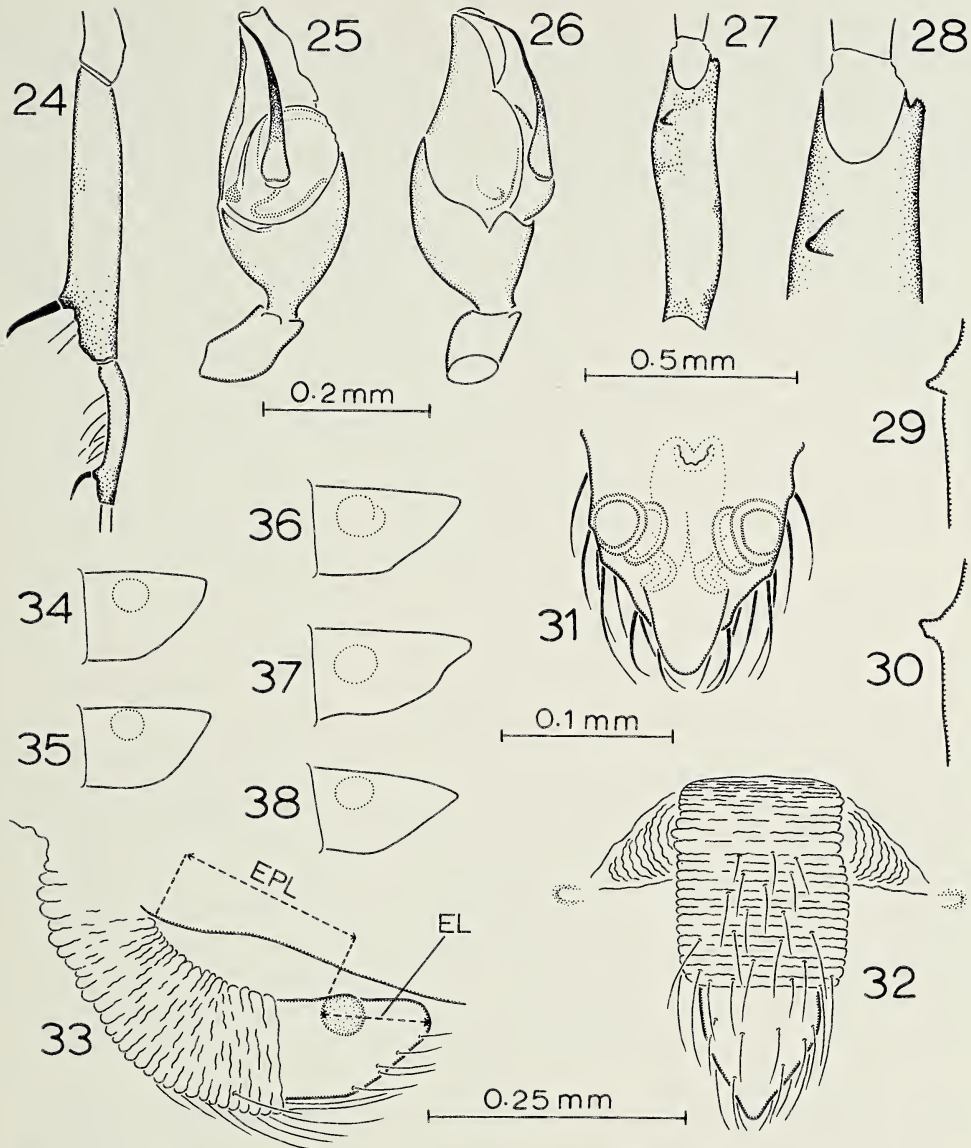
Distribution.—Known only from the type locality in the mountains of eastern Jamaica (Fig. 42).

Material examined.—Only the type specimens.

Mysmenopsis furtiva, new species

Figs. 4, 24-42

Types.—Male holotype and one female and two male paratypes collected in *Ischnothele* webs on hillside in dry limestone forest (approximately 300 m

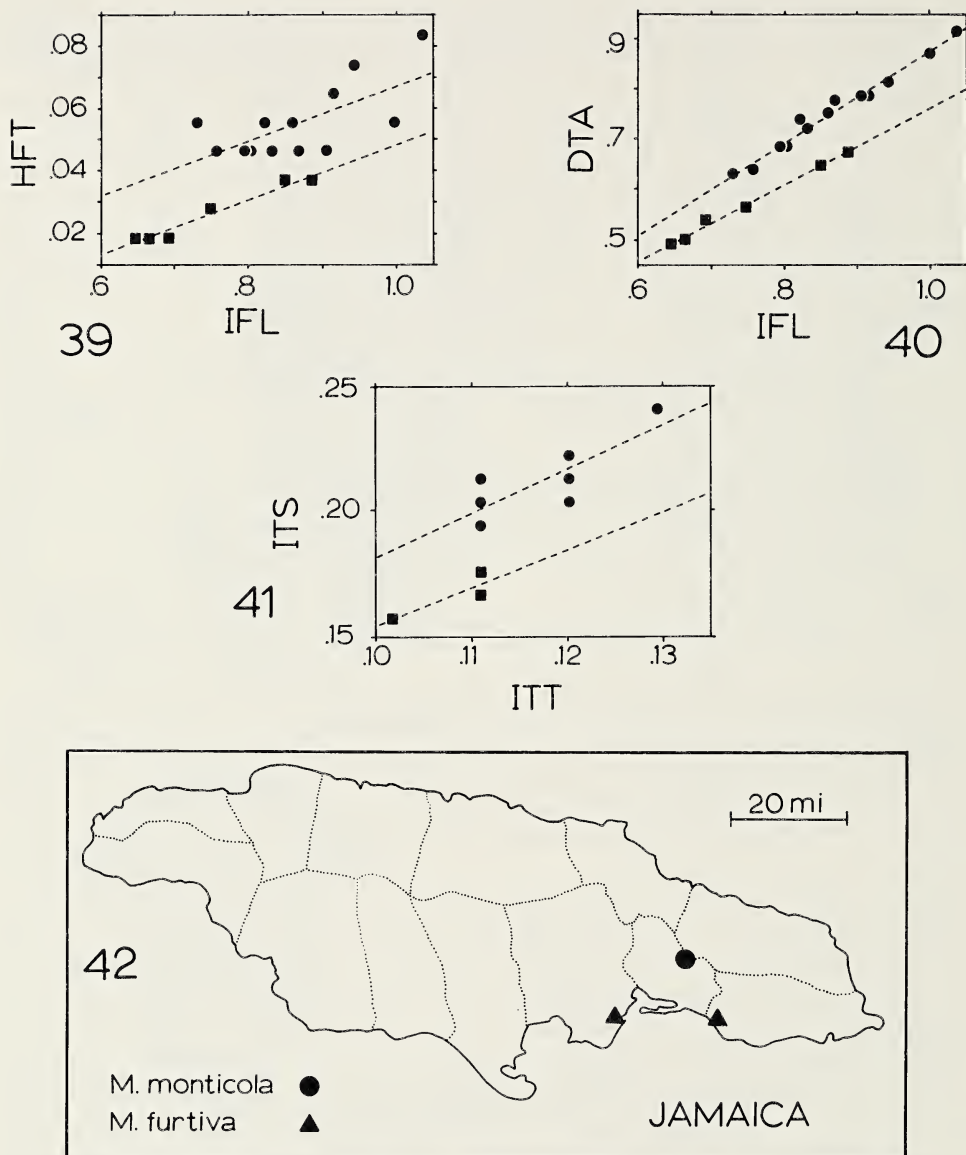


Figures 24-38.—*Mysmenopsis furtiva*: 24-26, holotype male; 24, tibia and metatarsus I, approx. prolateral; 25, 26, palp; 25, retrolateral; 26, ventral; 27-28, females; 27-29, 14 mi E Kingston; 27, 28, femur I, ventral; 29, 30, femur I ventral tubercle, view between ventral and retrolateral; 30, paratype; 31-38, epigyna; 31-33, paratype; 31, cleared, dorsal; 32, ventral; 33, lateral; 34-38, lateral view of five specimens, 14 mi E Kingston. Scale lines: 0.2 for Figs. 25, 26, 28-30; 0.5 for Figs. 24, 27; 0.1 for Fig. 31; 0.25 for Figs. 32-38.

elevation) 14-15 miles east of Kingston, St. Thomas Parish, Jamaica (10 April 1988; F. Coyle, R. Bennett, B. Freeman, and A. Robinson), deposited in the American Museum of Natural History.

Etymology.—The specific name refers to the stealthy, furtive nature by which these kleptoparasites are thought to procure food.

Diagnosis.—To distinguish *M. furtiva* from its close relatives, *M. monticola* and *M. tibialis*, refer to the diagnosis for *M. monticola*.



Figures 39-41.—Scattergrams for *Mysmenopsis monticola* (circles) and *M. furtiva* (squares) with regression lines (values in mm); 39, 40 females; 39, HFT vs. IFL (*M. monticola* regression: $y = 0.089x - 0.022$, $r = 0.673$; *M. furtiva* regression: $y = 0.089x - 0.041$, $r = 0.979$); 40, DTA vs. IFL (*M. monticola* regression: $y = 0.923x - 0.047$, $r = 0.989$; *M. furtiva* regression: $y = 0.767x - 0.006$, $r = 0.997$); 41, males, ITS vs. ITT (*M. monticola* regression: $y = 1.75x + 0.007$, $r = 0.810$; *M. furtiva* regression: $y = 1.5x + 0.005$, $r = 0.866$). Fig. 42.—Distribution of Jamaican *Mysmenopsis* species.

Males.—Table 1. Figs. 4, 24-26, 41. Palpal patella with sharp distal keel on retrolateral surface. Palpal tibia with ventral ledge produced into small lobe; no cusps associated with this ledge. Embolus with relatively narrow base; tapers gradually above base; unevenly curved (crooked) in ventral view; ending at distal edge of cymbium. Tibia I clasping spur attached to moderately short tubercle and bent distally. Legs with moderately dark patches on pale tan background; coxae mostly unpigmented; femur I with faint dark patches at proximal end, middle,

and near distal end; rest of femora with darker patches at each end and in middle; patellae with distal dark spot; tibiae with distal dark area and small dark spot in middle; metatarsi with distal dark spot; tarsi unpigmented. Overall, leg I lighter than other legs. Carapace and sternum moderately dark grey-brown. Abdomen with many areas of dark grey or black separated by areas of light grey with white spots; dorsally, two prominent, longitudinal, winding, light grey bands separated by dark central area except for two pairs of narrow median lobes of light grey which come moderately close to connecting at median line.

Females.—Table 2. Figs. 27-40. Distal half of femur I with small yet prominent ventral tubercle with steeply sloping proximal and distal faces, and angular apex; small, rough-surfaced tubercle on retrolateral surface at distal end of femur. Tibia I cylindrical. Metatarsus I without spines. Epigynum at end of long, narrow, unsclerotized, pleated lobe; tip with gentle distoventral slope and blunt, keel-like distodorsal prominence; hairs extend only slightly beyond tip; spermathecae consist of pair of oval chambers with a curved posterior median lobe on each side, and U-shaped, weakly sclerotized lip bordering opening on ventral surface of epigynum. Pigmentation similar to that of males.

Variation.—See the discussion of variation in *M. monticola* regarding the especially wide range of EPL variation in *M. furtiva*. Variation in epigynum shape and femur I tubercle shape is illustrated by Figs. 33-38 and 28-30.

Natural history.—The *M. furtiva* populations were found in much drier habitats than that occupied by *M. monticola* and its host. The Fort Clarence—Hellshire Hills population lived in a hot, dry, cactus thorn scrub community on limestone substrate with little soil. *Ischnothele* host webs at this site were usually found at the bases of rocks where leaf litter accumulates under the scattered small trees, and they were similar in size and shape to those occupied by *M. monticola*. The other *M. furtiva* population inhabited a dry forest community on a rocky (limestone) hillside. Here the host webs were most often found at the bases of rocks and exposed roots, their retreats penetrated the loose limestone pebble substrate, and they were much more abundant than in the cactus thorn scrub. At both sites individuals of *M. furtiva* were observed in several webs, always in the capture web near the retreat mouth. One female was observed carrying an egg sac.

Distribution.—Known from two localities along the south coast of eastern Jamaica (Fig. 42).

Material examined.—The type specimens and the following: JAMAICA: ST. CATHERINE PARISH; Fort Clarence and Hellshire Hills near Seafort, 10-50 m elevation, cactus thorn scrub, 9 April 1988 (F. Coyle, R. Bennett, B. Freeman, and A. Robinson), 5 females, several juvs. (AMNH).

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**SPINNERET SILK SPIGOT MORPHOLOGY:
EVIDENCE FOR THE MONOPHYLY OF ORBWEAVING SPIDERS,
CYRTOPHORINAE (ARANEIDAE),
AND THE GROUP THERIDIIDAE PLUS NESTICIDAE**

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ABSTRACT

Labelled scanning electron micrographs comprehensively illustrating the spinning fields of *Deinopis* (Deinopidae), *Octonoba* (Uloboridae), *Araneus* (Araneidae), *Leucauge* (Tetragnathidae), *Latrodectus* and *Theridula* (Theridiidae), *Gaucelmus* (Nesticidae), and *Frontinella* (Linyphiidae) are presented for the first time. Evidence from scanning electron micrographs supports the monophyly of orbweavers (Orbiculariae = Uloboridae, Deinopidae, Araneoidea), the araneid subfamily Cyrtophorinae and the close relationship between Nesticidae and Theridiidae. This evidence is presented in the context of guidelines for the logical taxonomic interpretation of spider spigot morphology. This morphological system, including gross and detailed morphology, location and number of spigots, and serial homology relationships, may be one of the most complex, yet under-utilized, taxonomic character systems in spiders.

INTRODUCTION

Spinnerets both define and epitomize spiders. The history of studies on spider silk glands has been reviewed by Kovoov (1977b). Despite her elegant studies (e.g., Kovoov 1972, 1977a, 1977c, 1988; Kovoov and Lopez 1982; Kovoov and Peters 1988), filled with interesting facts about peculiar spinneret morphologies, systematists rarely report on this diverse character system in their phylogenetic studies. Several explanations for this neglect suggest themselves, such as belief that histological evidence on glands is essential for interpretation of the morphology, or that one must fix living material to obtain satisfactory results. Perhaps the chief difficulty is that a detailed histological study is so time consuming that a large diversity of species within a taxon cannot easily be surveyed. Variation thus remains undocumented, and taxonomists remain uncertain about the constancy of a feature, and the pattern of its distribution. However, on close inspection, none of these objections are insuperable. This paper outlines how spigot morphology can be studied using ordinary museum material. It presents some of the more interesting results so far, and summarizes a conceptual framework for the interpretation of the data that, I hope, will encourage the use of spigot morphology in spider systematics.

In this study I present preliminary results from a larger study on silk spigot diversity in spiders in general. The taxa included herein have been chosen to illustrate how silk spigot characters may bear on particular systematic problems, and to illustrate the diversity of silk spigot morphology. The specific systematic problems discussed are the monophyly of orbweavers, the monophyly of Cyrtophorinae (*Cyrtophora* and *Mecynogea*, at least), and the monophyly of a group including Theridiidae and Nesticidae. Although the evidence in all three cases seems positive, one must be cautious until further taxa are surveyed.

I have previously reviewed the evidence for the monophyly of Araneoidea and Deinopoidea (=Uloboridae and Deinopidae; Coddington 1986a, b). The evidence formerly believed to support the polyphyly of orbweavers was largely due to a confusion between symplesiomorphy and synapomorphy—the misinterpretation of primitive features that “defined” the symplesiomorphic group “Cribellatae.” When the features that once defined the Cribellatae are recognized as primitive, there are no credible synapomorphies that place Deinopoidea with the rest of the cribellates, rather than with the other orbweavers (Araneoidea). On the contrary, most of the evidence implicates them as the sister taxon of the ecribellate Araneoidea. However, contrasting points of view have subsequently been expressed by Eberhard (1987), Shear (1986), Kooor and Peters (1988) and Tyshchenko (1986).

The monophyly of the Cyrtophorinae, on the other hand, although never explicitly justified, has rarely been doubted (Levi 1980, 1983; Levi and Coddington 1983). This paper offers evidence independent of genitalic morphology and web architecture to confirm cyrtophorine monophyly.

The composition of the Theridiidae has frequently been questioned, as well as its relationship to Nesticidae. For example, Lehtinen and Saaristo (1980) placed the latter two families in different superfamilies, mainly because of genitalic differences. In particular they suggested that the fourth tarsal comb of serrated bristles common to both families was “purely adaptive.” Palp and epigynal morphology among theridiids and nesticids obviously is diverse, but in any case offers no evidence to ally either group more closely with other araneoid taxa than with each other. However, the fourth tarsal comb is part of a behavior-morphology complex that enables nesticids and theridiids to subdue their prey with viscid sticky silk (Whitehouse 1987). This attack behavior is unique among spiders and stands as a strong synapomorphy of theridiids and nesticids (Coddington 1986a). This paper offers additional morphological evidence concordant with the fourth tarsal comb and the attack behavior itself. It is therefore additional evidence in favor of the monophyly of Nesticidae and Theridiidae.

This study also outlines the analytical methods one can use to deduce homologies among spigots, and thereby to use the data in phylogenetic analysis. Basically, Remane’s criteria of homology (position, special similarity, ontogeny) seem entirely adequate, and thus the comparative study of silk spigots can proceed to some extent independently of other lines of evidence, such as histology or histochemistry. This is not to say that the spigot evidence is superior to histological evidence, but only that the morphology and exact location of araneomorph spigots seems complex enough and consistent enough to support generalizations. Histology is not *required* in order to infer spigot homologies. Spigot morphology may even help to decide questions of homology when the

histological evidence is equivocal. Indeed, when patterns in histological and histochemical data (e.g., Kovoov 1987) are compared with well-corroborated groups in spider phylogeny, many details of histochemical reactions, gland ultrastructure, and gland cell type are apparently homoplasious (see Discussion).

MATERIALS AND METHODS

Spigot morphology is extremely difficult to see with light microscopy. If one must use the light microscope, the best results are obtained with epi-illumination, but even then distinctive details are easy to miss (e.g., Mikulska 1966, 1967; Wasowska 1966, 1970). No doubt that helps to explain the neglect of spigot morphology as a character system in the past. However, the increasing availability of scanning electron microscopes (SEM) puts study of spigot morphologies well within the grasp of most spider taxonomists.

The best preparations have the spinnerets widely spread, are clean, and can be scanned from all angles. Several workers with whom I have spoken have had difficulties in getting good results, usually because the spinnerets are contracted upon themselves so that the distal articles cannot be seen, or else the spigots are covered with debris. In this study, these obstacles were overcome with good success by the following techniques.

Selection of material.—Obviously fresh material is best, although I have successfully prepared 50-100 year old specimens. If live material is available, kill the animals by direct, sudden immersion in boiling water or fixative. Under these conditions, the spinnerets are widely spread. In the case of ordinary museum material, the only real requirements are an intact set of spinnerets and a flexible abdomen. The latter is important in case the spinneret tips need to be spread. However, even hardened material can be used if one digests the spinneret group in a trypsin solution prior to mounting. All the material here is from the USNM collection, and voucher specimens are deposited there. Except in one case, only adult females were used.

Forceps squeeze.—As long as the abdomen of the specimen is still flexible, the spinnerets can be spread with forceps. This technique has been modified from one originally suggested by Dr. J. Kovoov. One must use cross-action forceps or otherwise be able to lock them in a closed position. One can use a rubber band around the forceps blades, or a wire collet that can slide forward to lock the tips. By experimenting with various angles, one can usually squeeze the abdomen immediately above (dorsal or anterior to) the spinnerets so that all six spinnerets spread widely. At this point, lock the forceps shut, sever the spinnerets from the abdomen with a razor, and run the spinnerets through an alcohol series up to anhydrous ethanol while they are still grasped by the forceps. Dehydration stiffens the spinnerets so that one can remove the forceps and the spinnerets will stay in a spread position. At this point, they are ready for cleaning.

If the forceps technique does not separate the spinnerets, sever the spinneret group and digest it completely in trypsin solution. This removes all muscle tissue and leaves only the cuticle of the spinneret group, so that it will be flexible enough to spread the spinnerets during the mounting process.

Ultrasonic cleaning.—Immersing the spinnerets (still gripped in the forceps) in an ultrasonic cleaner for 1-10 minutes will remove debris. If the specimen is

extremely fragile (e.g., Ochyroceratidae, Nesticidae, Symphytognathidae), decrease the time. Clean spigots are distinctly visible at 100X. Special care must be taken to clean trypsin-digested spinnerets. Brief soaking in 10% KOH to remove enzymatic protein is often helpful.

Stub mounting.—The cleaned, spread spinneret group is now ready to be mounted. One must use a stub so that the spinneret group can be rotated into nearly any angle for viewing. Standard, disc-shaped SEM stubs do not work well because the stub edge obscures the view or ruins the background contrast. I use 1/8 in. diameter steel rivets. The hemispherical head permits an unobstructed view of the spinnerets from any angle, and one can tip the stub to a 90° position so that the SEM background will be completely black. Spinnerets prepared by the forceps technique can be mounted with the usual adhesives, such as silver paint.

Trypsin-digested spinnerets that require spreading should be mounted with a stickier adhesive, such as the gum from double stick tape. In this case, the cured surface of the rivet anchors the outer edge of the cuticle, and by careful additional pushing and denting of the cuticle surface, one can spread the spinneret tips at this point.

RESULTS

Figure 1 diagrams the typical distribution of spigots in an araneoid spider. Figures 2-41 illustrate the diversity of spigots in *Deinopis* (Deinopidae), *Octonoba* (Uloboridae), *Araneus* (Araneidae), *Leucauge* (Tetragnathidae), *Cyrtophora* and *Mecynogea* (Araneidae: Cyrtophorinae), *Latrodectus* and *Theridula* (Theridiidae), *Gaucelmus* (Nesticidae), and *Frontinella* (Linyphiidae). Spigots in all figures are labelled in accordance with Table 1. Each plate of figures is laid out the same way. The upper left micrograph shows the left three spinnerets. Anterior is always at the top. The upper right micrograph shows the left ALS (anterior lateral spinneret) tip; the lower left micrograph the left PMS (posterior median spinneret) tip; and the lower right micrograph the left PLS (posterior lateral spinneret) tip. In the three close-up micrographs anterior is usually at the top or left, but if not, the orientation can be figured out by referring to the upper left micrograph. Abbreviations of spinneret and spigot terminology are given in the legend to Figs. 2-5. Spigots in Figs. 2-9 are labelled with arrows for precision, thereafter the labels are adjacent to the spigots.

Deinopoidea.—The cribellate *Deinopis* and *Octonoba* illustrate the orb-weaver ground plan. The piriform spinning field is more or less uniformly distributed across the ALS tip (Figs. 3, 7; PI). The major ampullate spigot(s) is (are) on the mesal margin of the ALS (Figs. 3, 7; MAP). Like the Araneoidea, adult female *Octonoba* have one functional major ampullate spigot, bordered posteriorly by a vestigial nubbin (also diagrammed in Fig. 1), presumably the remainder of the second MAP present in juveniles. *Deinopis* have multiple MAPs, a fairly rare feature among araneomorph spiders. The cuticle sculpturing is grooved and fluted (see also Kovoov and Peters 1988), apparently a synapomorphy for Neocribellatae.

The posterior median spinneret of *Octonoba* shows four classes of spigots. There are three cylindrical spigots and one posterior minor ampullate spigot (Fig.

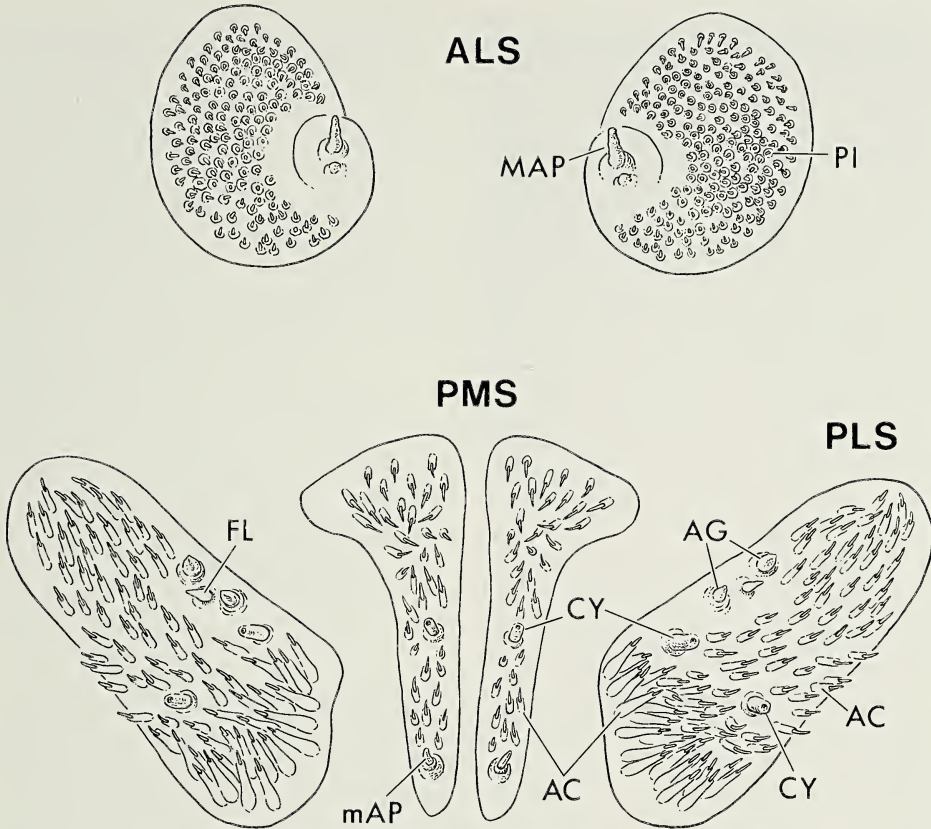


Figure 1.—Generalized araneoid spinneret and spigot location.

8; CY, mAP). Around and between them is a group of many (>30) small aciniform spigots (Fig. 8; AC), which extend forward on to the anterior wall of the PMS spinneret. Finally, there is an anterior brush of many elongate, annulated, paracribellar spigots (Fig. 8; PA). The condition in *Deinopis* is similar, although they seem to have many more cylindrical gland spigots than uloborids (Fig. 4; CY).

The posterior lateral spinneret is also complex. On the mesal basal margin in *Octonoba* are six cylindrical spigots (Fig. 9; CY). On the anterolateral margin is the pseudoflagelliform spigot (Fig. 9; PF). Distributed across the face of the PLS are a second group of aciniform spigots (Fig. 9; AC). Figure 5 shows a *Deinopis* immature female—thus she lacks all cylindrical spigots, and has only the pseudoflagelliform and aciniform spigots (Fig. 5; PF, AC). Adult female *Deinopis*, like other deinopoids, have multiple, basal, cylindrical gland spigots on the PLS.

Araneoidea.—The spinning fields of *Araneus* illustrate the rather conservative and consistent araneoid ground plan. The cuticle sculpturing is lenticular or squamate, rather than fluted or grooved. That feature, of course, is found in other spider taxa than Araneoidea. As in Deinopoidea, the piriform spinning field is uniform across the ALS tip (e.g., Figs. 11, 23, 27, 31, 35, 39; PI). This condition has been distinctively modified in *Mecynogea* and *Cyrtophora*, however, whose piriform field has been restricted posteriorly to a ribbon (Figs.

Table 1.—Orbweaver silk spigots categorized by number (singular or multiple), the glands they presumably serve, and position in the spinneret field.

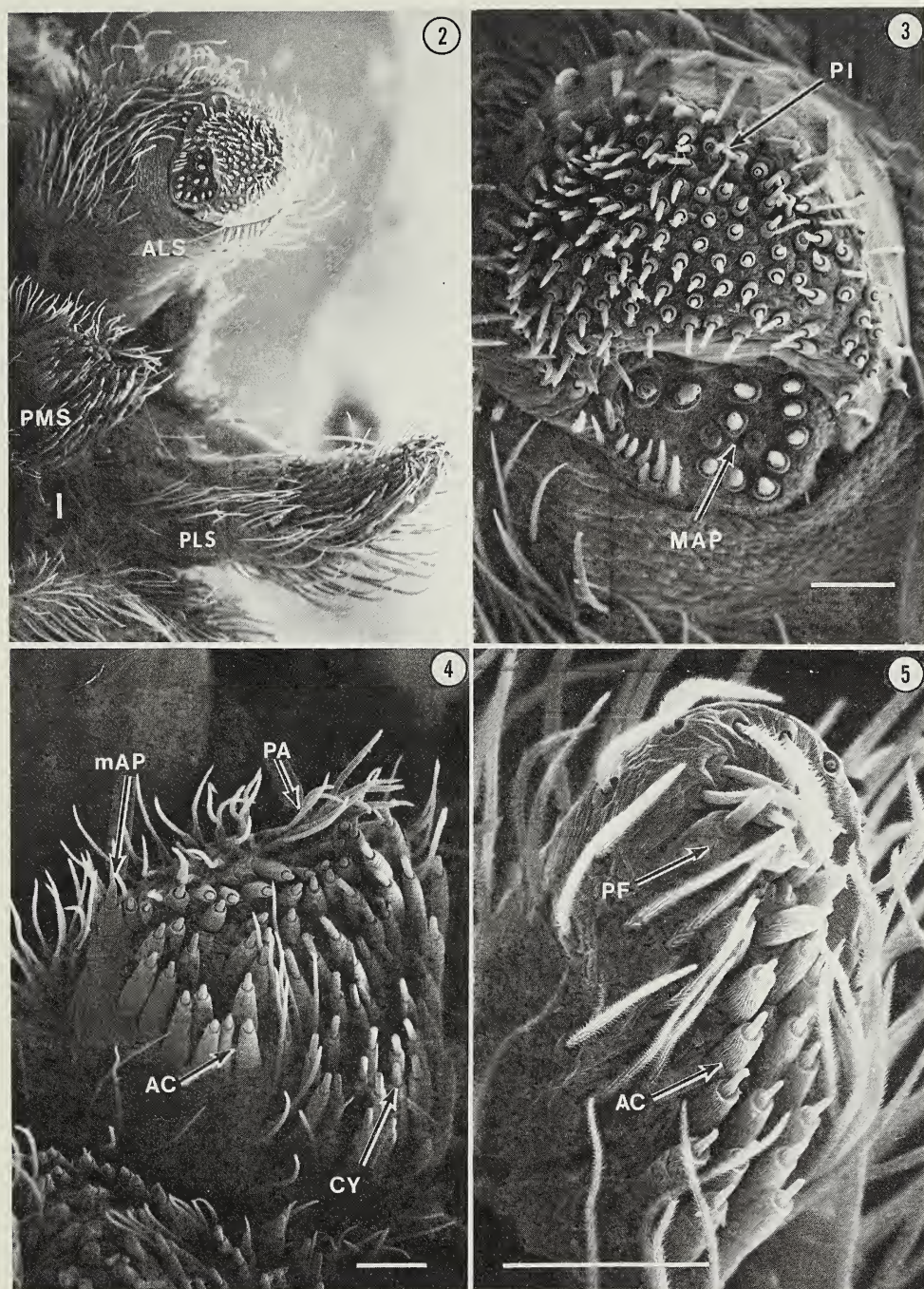
Spigot type	Position/Description
SINGULAR	
1. Major ampullate	A single spigot on the mesal border of the ALS. Present in most if not all araneomorphs.
2. Minor ampullate	A single spigot on the posterior margin of the PMS. Present in most if not all araneomorphs.
3. Cylindrical	In Araneoidea, 3 spigots: 2 on basal margin of PLS tip and 1 on anterior margin of PMS. Number varies in other groups, but apparently always on PMS and PLS.
4. Flagelliform	In Araneoidea, a unique spigot between the aggregate spigots of the PLS.
5. Pseudoflagelliform	One spigot on the antero-lateral margin of the PLS in some cribellate spiders; homologue of the flagelliform in araneoids?
6. Aggregate	In Araneoidea, two similar spigots near the flagelliform spigot.
MULTIPLE	
7. Piriform	A group of small apiculate spigots on the ALS. Present in most if not all araneomorphs; morphology but not position variable.
8. Aciniform	The most numerous gland type; small spigots present in multiples on PMS and PLS. Present in most if not all araneomorphs; morphology variable.
9. Paracribellar	A group of long, thin, often annulated spigots on the anterior PMS margin in some cribellate spiders.

15, 19; PI). The major ampullate spigot with its vestigial partner is on the mesal margin of the ALS in all the araneoids (Figs. 11, 15, 19, 23, etc.; MAP).

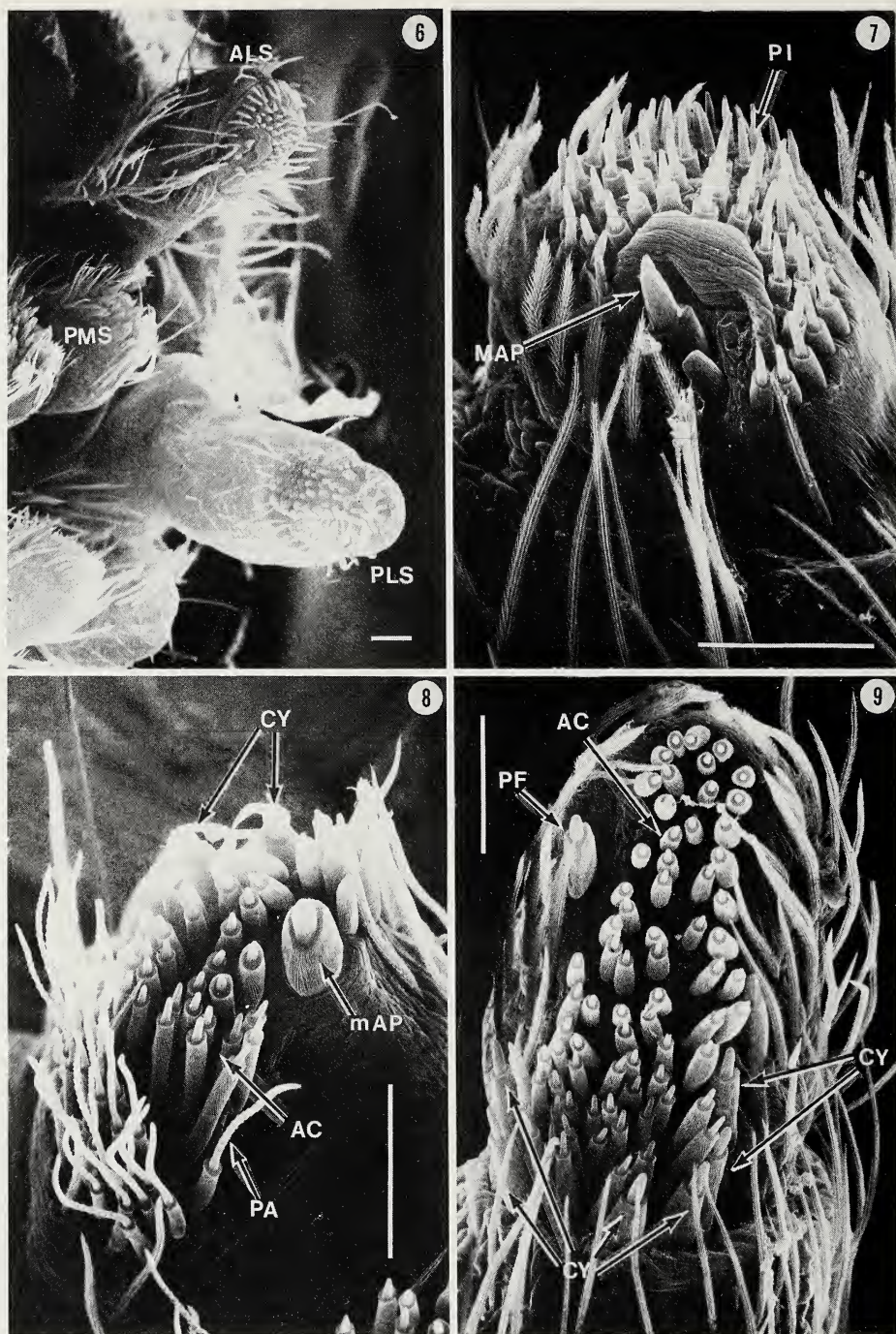
The posterior median spinneret shows three classes of spigots: the single anterior cylindrical spigot, the single posterior minor ampullate spigot, and the surrounding and/or intervening group of many small aciniform spigots (Figs. 12, 16, 20, 24, 28, 32, 36, 40; CY, mAP, AC, respectively). In *Araneus* (Fig. 12), *Mecynogea* (Fig. 16), and *Cyrtophora* (Fig. 20), as in cribellate orbweavers, the aciniform spigot field extends forward on the anterior wall of the spinneret. The restriction of the PMS aciniform field to the spinneret tip, or at least its absence from the anterior face in *Leucauge* (Fig. 24), and other derived araneoids such as theridiids (Figs. 28, 32), nesticids (Fig. 36), and linyphiids (Fig. 40), is a derived condition. *Leucauge*, *Latrodectus*, and *Gaucelmus* have just three aciniform spigots, *Theridula* and *Frontinella* (as well as other linyphiids) have only two.

In Araneoidea, the posterior lateral spinneret is the most complex. On its mesal basal margin are two cylindrical spigots (e.g., Figs. 13, 25; CY), although their position sometimes shifts (e.g., *Frontinella*, Fig. 41). On the anterolateral margin is the flagelliform, and the two aggregate glue gland spigots (e.g., Figs. 13, 25, 41; FL, AG). Distributed across the PLS tip is a second group of aciniform spigots (e.g., Figs. 17, 21; AC). The PLS flagelliform-aggregate complex in *Cyrtophora* is entirely absent, whereas it is merely reduced in *Mecynogea* (compare Figs. 17, 21 with "normal" spigots in *Araneus*, Fig. 13, or *Frontinella*, Fig. 41).

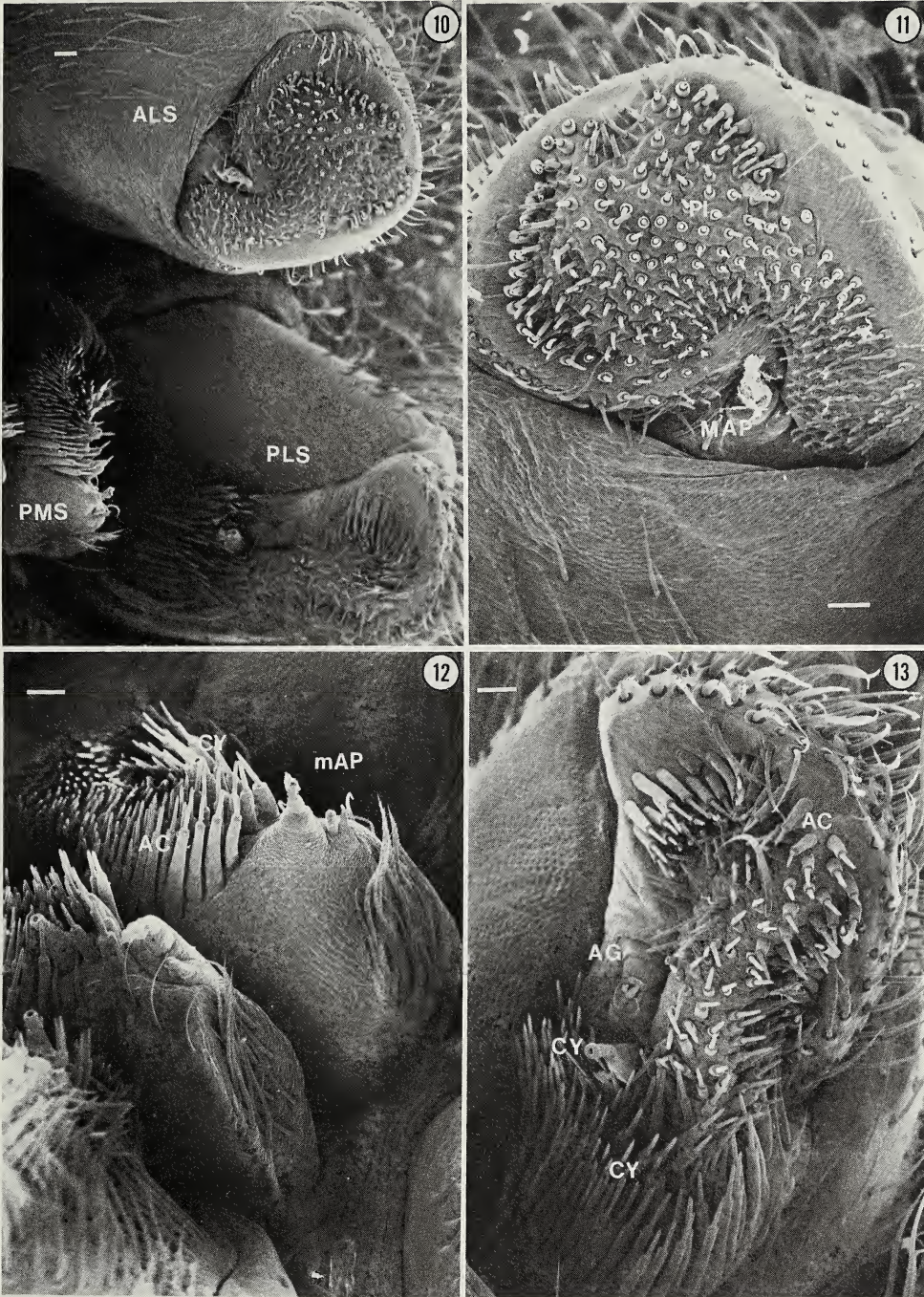
The theridiid and nesticid complements are also modified, but in a different way. On the theridiid PLS, the two aggregate glands are relatively enormous, the ectal larger than the mesal (e.g., *Latrodectus*, *Theridula* Figs. 29, 33; AG). The same situation occurs in nesticids, although the difference between the two



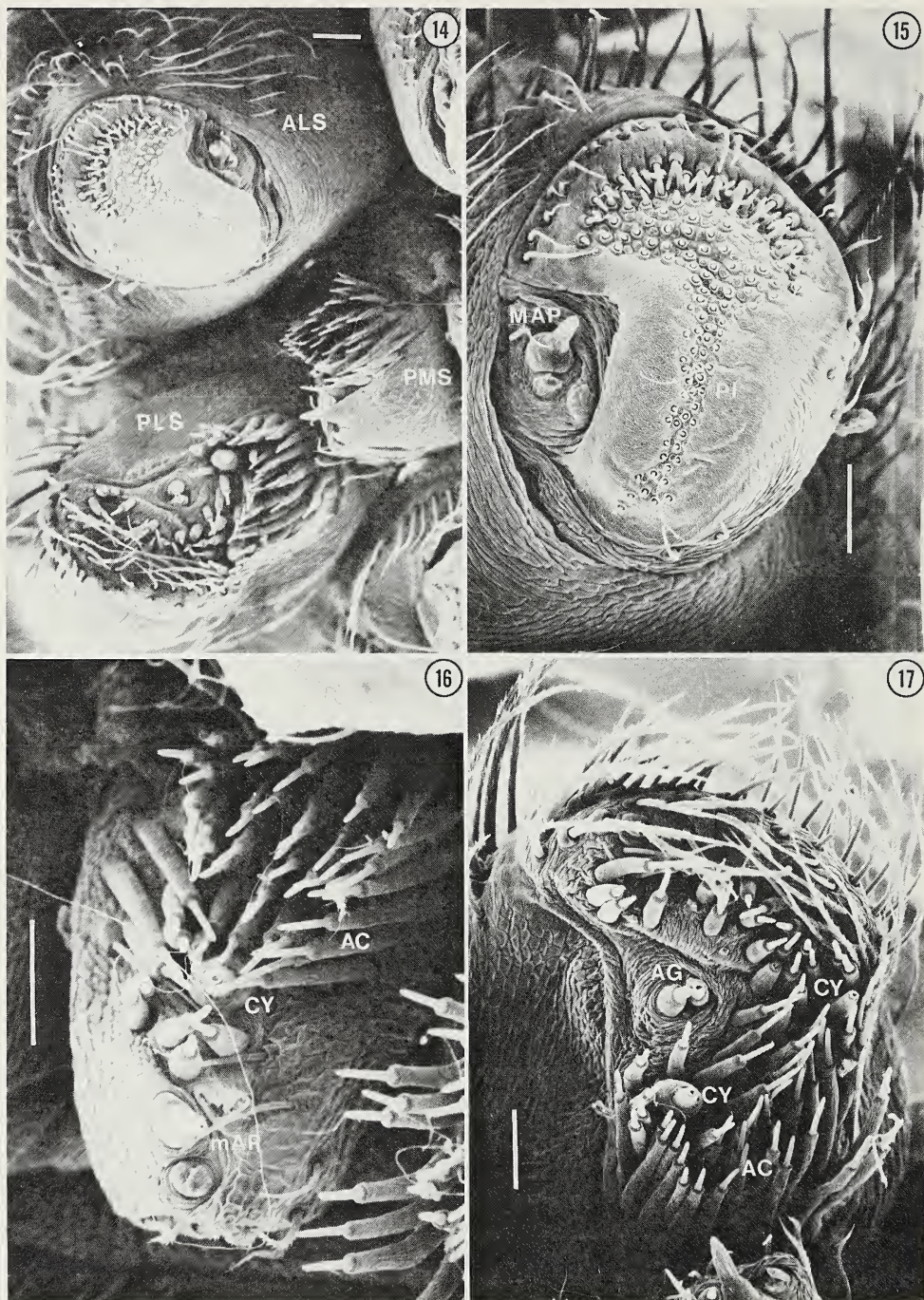
Figures 2-5.—*Deinopis spinosus* Marx spinnerets: 2, left spinneret group; 3, anterior lateral spinneret, closeup; 4, posterior median spinneret, closeup (subadult female); 5, posterior lateral spinneret, closeup. Abbreviations for Fig. 1-41: AC = aciniform; AG = aggregate; ALS = anterior lateral spinneret; FL = flagelliform; MAP = major ampullate; mAP = minor ampullate; CY = Cylindrical; PA = paracribellar; PF = pseudoflagelliform; PI = piriform; PMS = posterior median spinneret; PLS = posterior lateral spinneret. Scale bars = 50 μ m.



Figures 6-9.—*Octonoba octonarius* (Muma) spinnerets: 6, left spinneret group; 7, anterior lateral spinneret, closeup; 8, posterior median spinneret, closeup; 9, posterior lateral spinneret, closeup. Abbreviations as in Figs. 2-5. Scale bars = 50 μ m.



Figures 10-13.—*Araneus diadematus* Clerck spinnerets: 10, left spinneret group; 11, anterior lateral spinneret, closeup; 12, posterior median spinneret, closeup; 13, posterior lateral spinneret, closeup. Abbreviations as in Figs. 2-5. Scale bars = 50 μ m.



Figures 14-17.—*Mecynogea lemniscata* (Walckenaer) spinnerets: 14, left spinneret group; 15, anterior lateral spinneret, closeup; 16, posterior median spinneret, closeup; 17, posterior lateral spinneret, closeup. Abbreviations as in Figs. 2-5. Scale bars = 50 μ m.

aggregate spigots is not as pronounced (*Gaucelmus*, Fig. 37; *Nesticus* and *Eidmanella*, not figured). In addition, the aciniform spinning fields on the PMS are much reduced in comparison with araneids, and are limited to the posterior and apical surface of the spinnerets.

DISCUSSION

Spigot homologies.—The above results argue that by judicious use of spigot number, placement, appearance, and known ontogenetic patterns, one can often work out spigot homologies without reference to histological data. A basic rule of inference is the difference between morphological singulars and multiples, or homologues and homonyms (Riedl 1979). Morphological singulars are unique and can be exactly specified, such as “the left third tarsus”, or, in this case, “the basal cylindrical gland of the PLS.” On the other hand, morphological “multiples” are present in many copies and are not individually specifiable, such as “abdominal setae,” or, in this case, the “aciniform spigots of the PMS.” One can make exactly specifiable homology statements about morphological singulars, but usually one can only homologize groups or sets of morphological multiples. In the case of spigots one has both singulars, such as major ampullates, minor ampullates, cylindricals, pseudoflagelliforms, aggregates and flagelliforms, and “multiples,” such as paracribellars, piriforms, and aciniforms. When multiple spigots are reduced in number, they may be consistent enough in their distributions to support hypotheses of individual homology (compare aciniform spigots in Figs. 4, 8, 12 vs. Figs. 28, 32, 36, 40). In combination with their placement, the distinction between singulars and multiples offers a way to tell the different kinds of spigots apart.

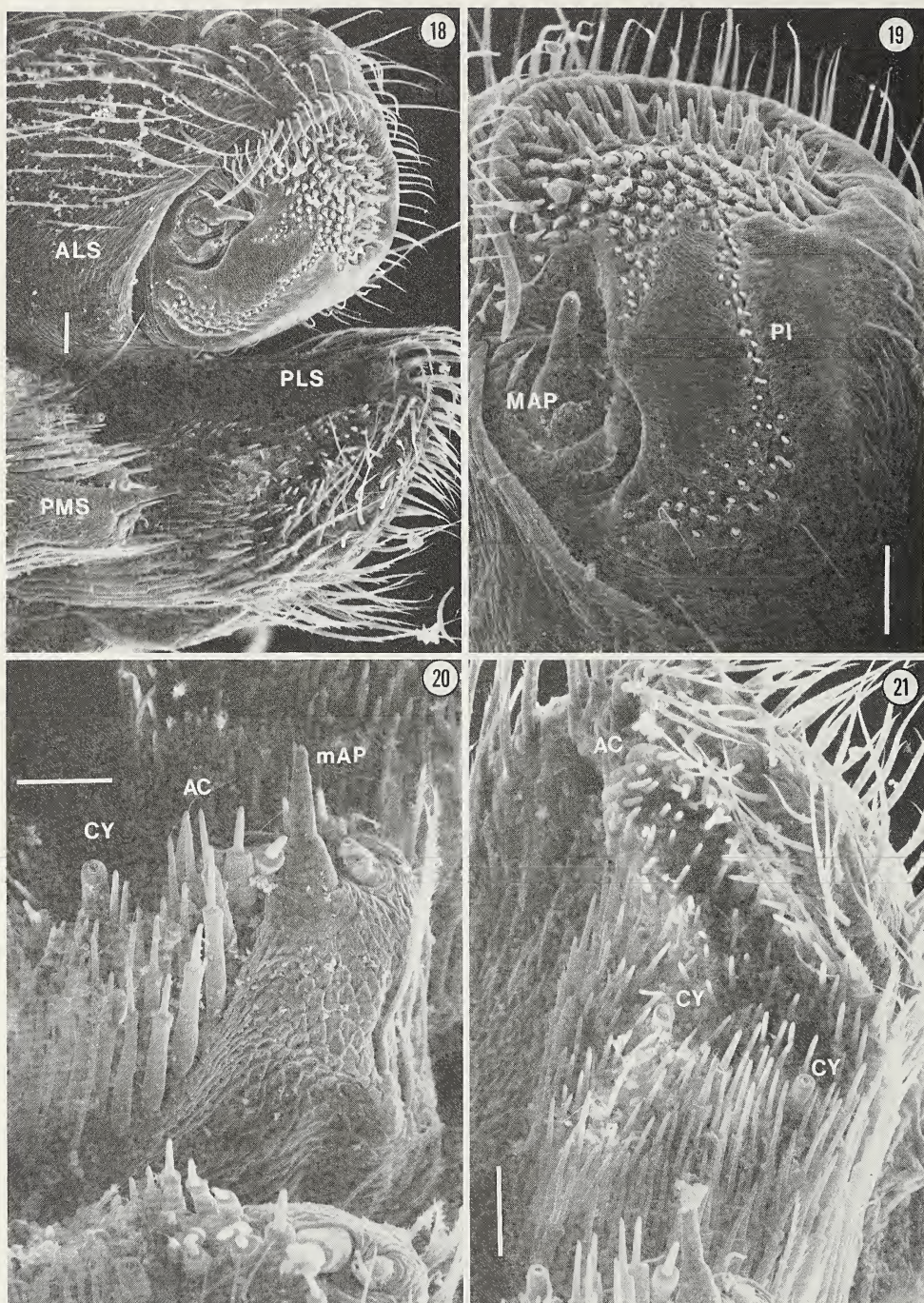
By trading off similarities between singular spigots, groups of spigots, and where they occur, one can devise a set of rules to guide homology statements about spigots, at least within the orbweavers. They can be summarized as follows:

MULTIPLES

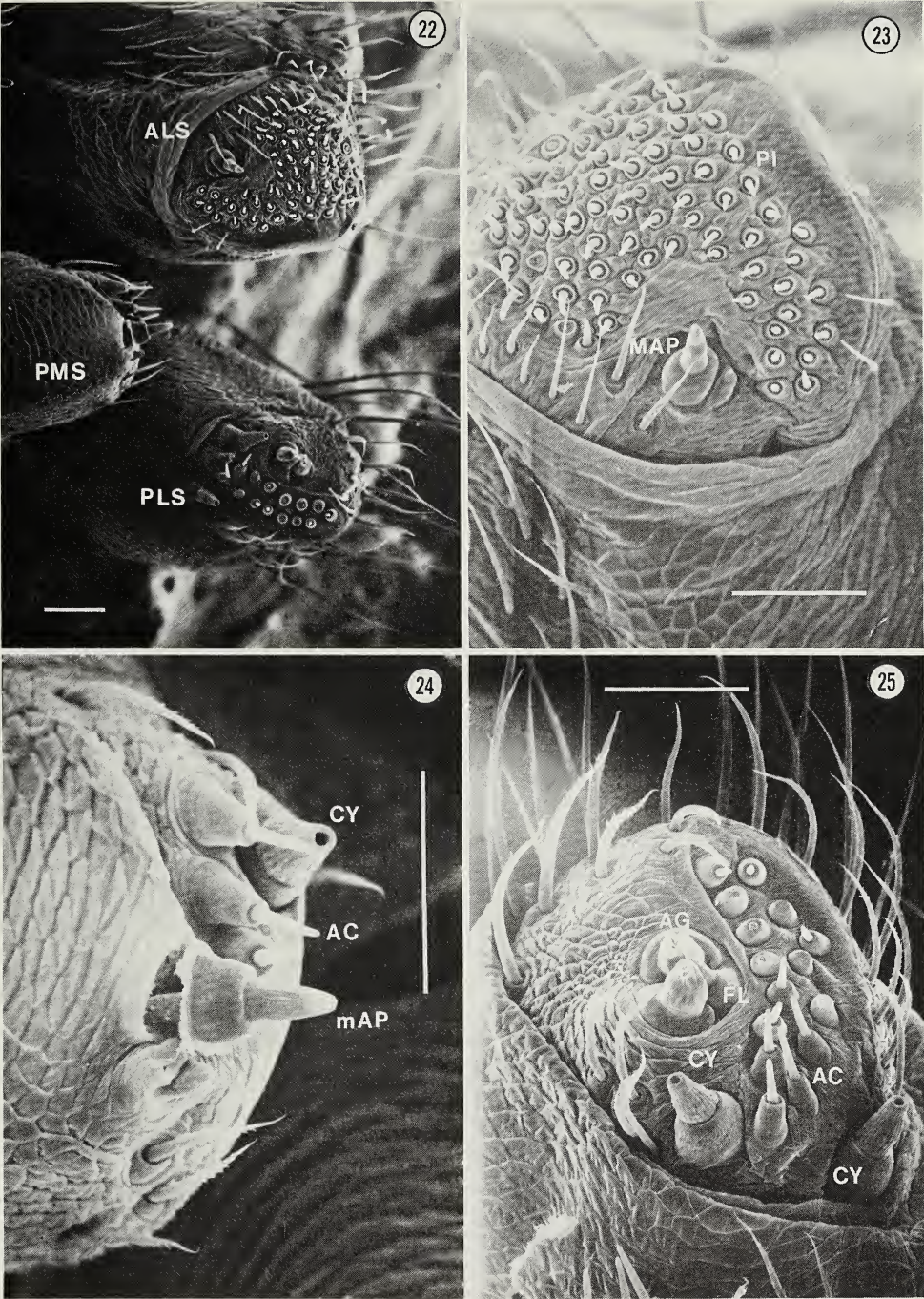
1. If the spigots are unique to the ALS and are small, numerous, and occupy most of the ectal spinning field, they are *piriform gland spigots*. They are used to attach draglines together or to the substrate. They should occur in all instars and both sexes.
2. If they occur both on the PMS and PLS and are small, but slightly more elongate than the ALS piriforms, they are probably *aciniform gland spigots*. They have several uses: prey wrapping, retreats, and egg sacs. They should occur in all instars and both sexes.
3. If they occur only on the PMS and are thin, very long, and with annulate shafts, they are probably *paracribellar spigots*. Their function is unclear, although they contribute a component to the sticky thread. They should occur in all instars and both sexes of all cribellate orbweavers, at least.

SINGULARS

4. If a set of three spigots occur as two on the araneoid PLS and one on the anterior portion of the araneoid PMS, they are *cylindrical gland spigots*. They are apparently used to produce specialized silk for egg sacs. They



Figures 18-21.—*Cyrtophora citricola* (Forskål) spinnerets: 18, left spinneret group; 19, anterior lateral spinneret, closeup; 20, posterior median spinneret, closeup; 21, posterior lateral spinneret, closeup. Abbreviations as in Figs. 2-5. Scale bars = 50 μ m.



Figures 22-25.—*Leucauge venusta* (Walckenaer) spinnerets: 22, left spinneret group; 23, anterior lateral spinneret, closeup; 24, posterior median spinneret, closeup; 25, posterior lateral spinneret, closeup. Abbreviations as in Figs. 2-5. Scale bars = 50 μ m.

should only occur in adult females. The situation in cribellate orbweavers is more complex because more cylindricals are present, but their distribution is as in araneoids.

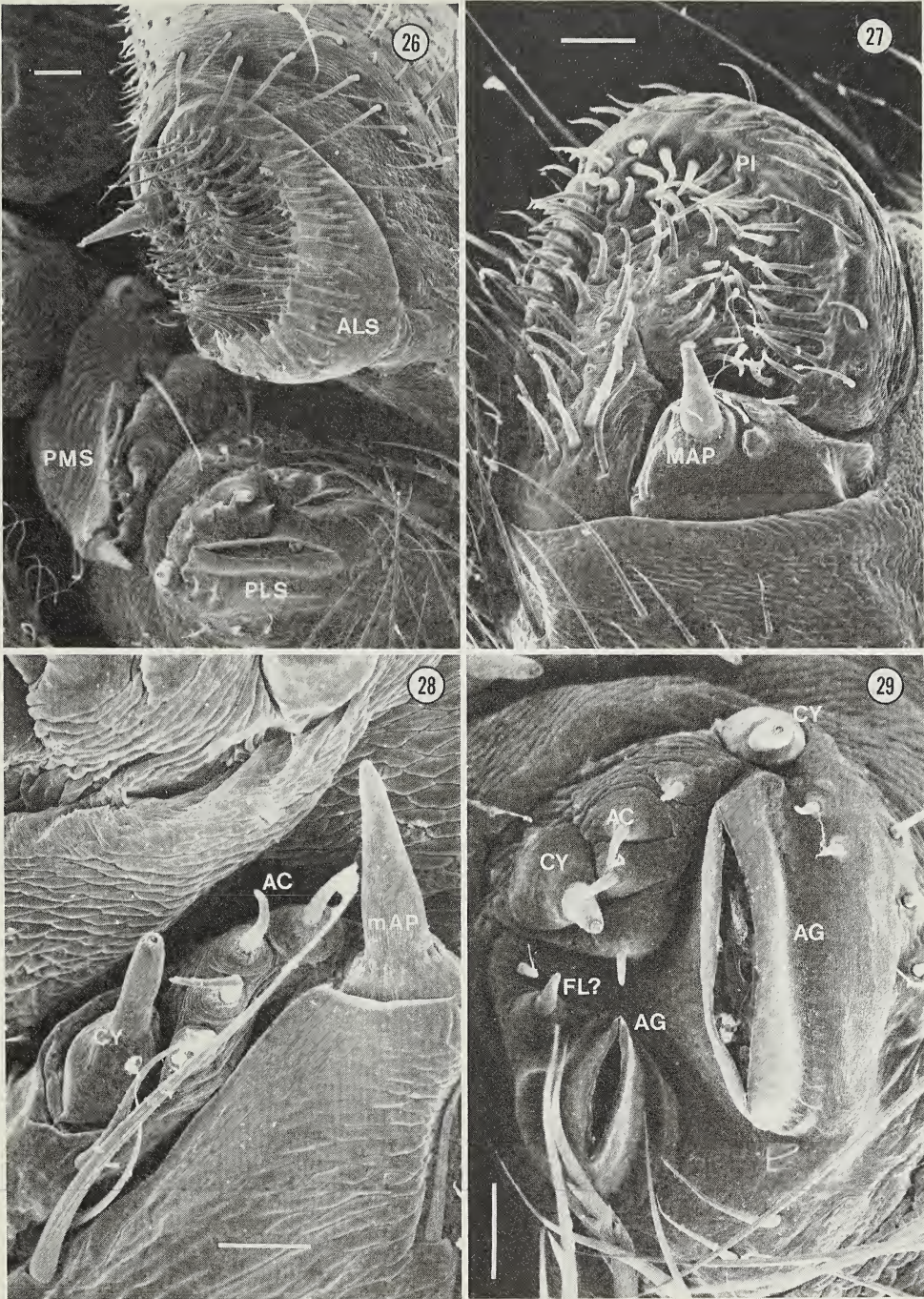
5. If a pair (or group, Deinopidae) of spigots occur as one on the mesal margin of the ALS and one on the posterior margin of the PMS, they are *ampullate gland spigots*, usually one major and one minor. They are used for components of the dragline and major structural lines. They should occur in all instars and both sexes.
6. If a pair of large spigots with wide openings is juxtaposed on the anterolateral margin of the PLS, they are *aggregate gland spigots*, used to make the viscid glue of the sticky line. They should occur in juveniles and adult females, but are supposed to be absent in all adult males (exceptions may occur).
7. If a single large spigot is unique to the PLS anterolateral or apical margin, it is the *flagelliform* or *pseudoflagelliform gland spigot*, used to make the base fibers of the sticky line. Flagelliform spigots are usually between the two aggregate spigots, but not always. Like the aggregate gland spigots, flagelliform and pseudoflagelliform spigots should occur in juveniles and adult females, and should be absent in adult males.

These rules were used to identify the various spigots present in the genera illustrated here. Of these, only *Araneus*, *Latrodectus*, *Cyrtophora* and *Mecynogea* have been studied histologically (Kovoor 1972, 1977a, 1988; Kovoor and Lopez 1982, 1988), but no SEM illustrations of them have been published. As far as I know, only the spinnerets of *Nephila* among the araneoids have been comprehensively illustrated (Kovoor 1986), although details of spigots of several uloborids have been published (Peters and Kovoor 1980; Kovoor and Peters, 1988).

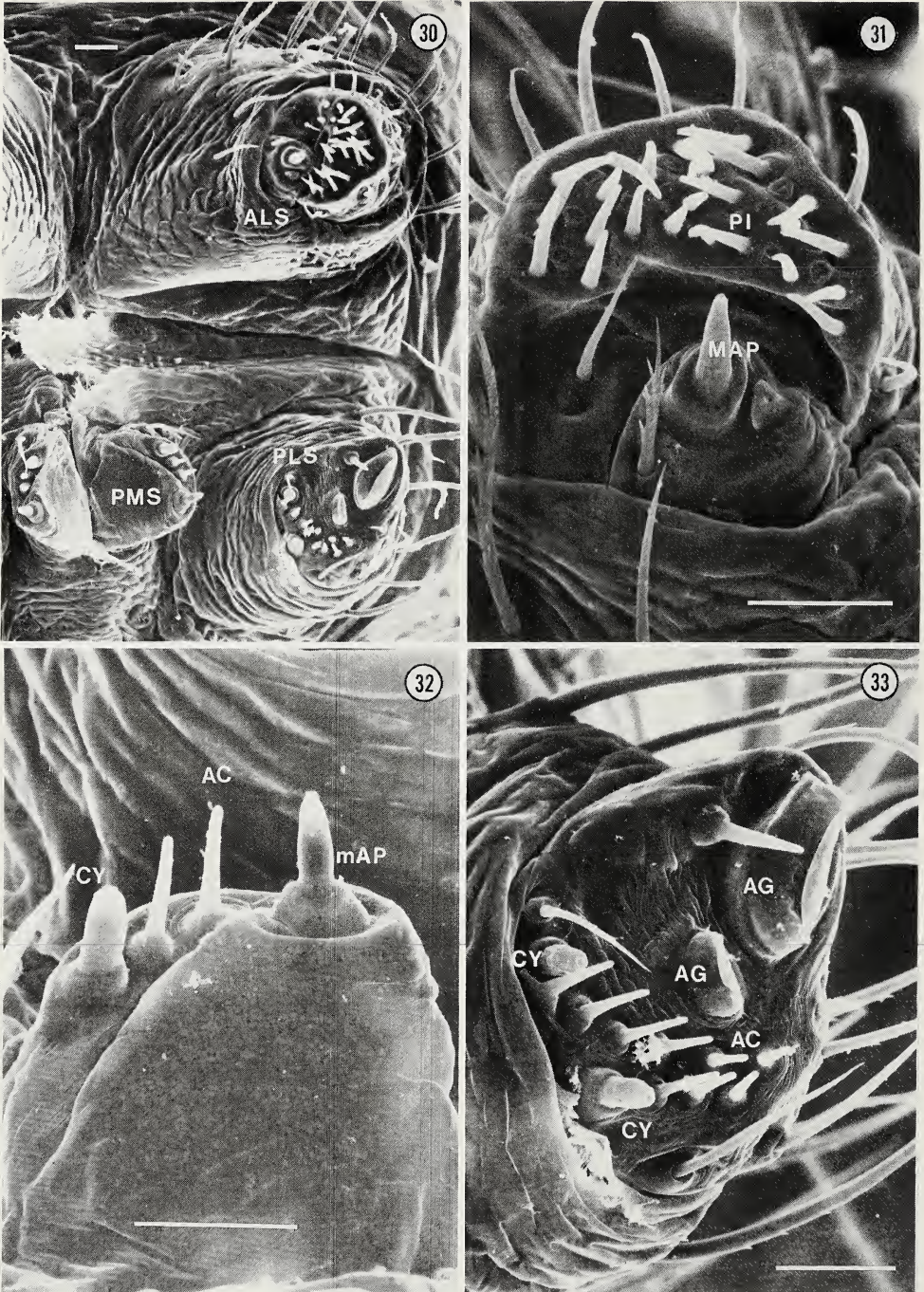
As an example one can use the above set of rules to correlate the large spigots on *Leucauge* PMS with known gland types. Because they are few in number, and are individually recognizable, they are probably examples of morphological singulars. Cylindrical glands exit on the PMS and PLS (#4, above). Araneoid ampullate glands exit only on the ALS and the PMS (#5, above). In Figs. 24-25, *Leucauge* has three large spigots with broad bases, sharply tapering, fluted, blunt shafts, and wide tips. The junction between the base and the shaft has a narrow indistinct rim. One of these spigots exits on the PMS (Fig. 24, CY), and two on the PLS (Fig. 25, CY). Therefore, they probably serve cylindrical glands.

Likewise, the major ampullate gland on the *Leucauge* ALS is similar to the spigot labelled as the minor ampullate gland on the PMS (Fig. 24, mAP). One can thus homologize spigots on orbweaving spiders, for example between *Leucauge*, a tetragnathid, and *Frontinella*, a linyphiid, even without histological evidence in these particular cases.

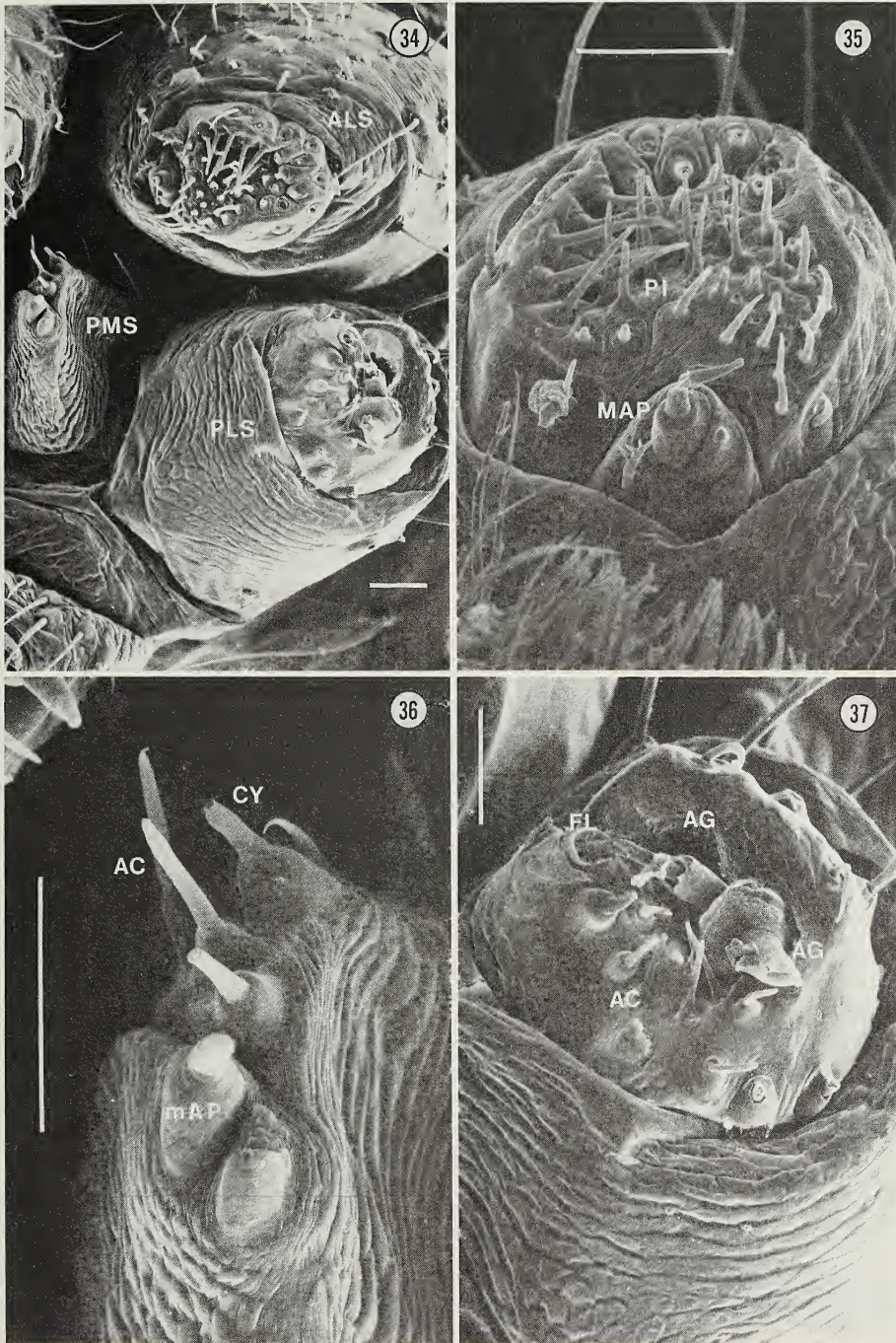
As an example of morphological multiples, piriform spigots are the only set of multiple spigots on the araneoid ALS tip. They are easy to recognize. However, in more distantly related groups, such as Deinopidae, two sets of multiples occur on the ALS. Only one set is on the mesal margin, set apart from the rest of the spinning field, and it is less numerous, and the spigots are larger. Because they occur in the same place as major ampullate glands, one can guess that they are indeed ampullate glands, and that Deinopidae is derived in having multiple ALS



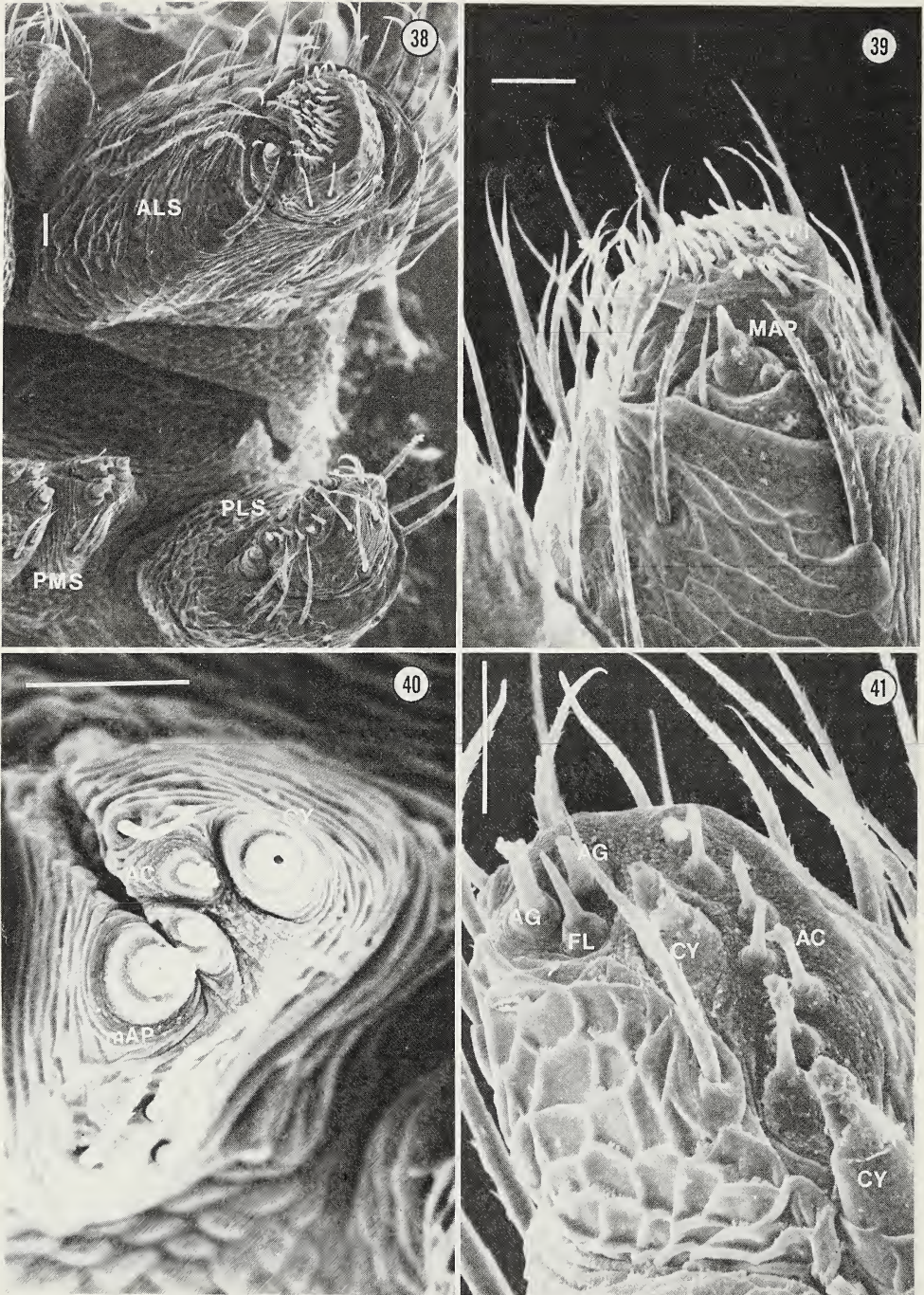
Figures 26-29.—*Latrodectus variolus* (Walckenaer) spinnerets: 26, left spinneret group; 27, anterior lateral spinneret, closeup; 28, posterior median spinneret, closeup; 29, posterior lateral spinneret, closeup. Abbreviations as in Figs. 2-5. Scale bars = 50 μ m.



Figures 30-33.—*Theridula opulenta* (Walckenaer) spinnerets: 30, left spinneret group; 31, anterior lateral spinneret, closeup; 32, posterior median spinneret, closeup; 33, posterior lateral spinneret, closeup. Abbreviations as in Figs. 2-5. Scale bars = 20 μ m.



Figures 34-37.—*Gaucelmus angustinus* Keyserling spinnerets: 34, left spinneret group; 35, anterior lateral spinneret, closeup; 36, posterior median spinneret, closeup; 37, posterior lateral spinneret, closeup. Abbreviations as in Figs. 2-5. Scale bars = 50 μ m.



Figures 38-41.—*Frontinella pyramitela* (Walckenaer) spinnerets: 38, left spinneret group; 39, anterior lateral spinneret, closeup; 40, posterior median spinneret, closeup; 41, posterior lateral spinneret, closeup. Abbreviations as in Figs. 2-5. Scale bars = 20 μ m.

ampullate glands. This may be a synapomorphy for the family (it also occurs in *Menneus*, pers. obs.). By position and morphology, the other group of smaller multiples on the deinopid ALS are therefore the piriforms. By similar logic, one can also guess that deinopids are strange in having up to 50 pairs of cylindrical gland spigots (Fig. 4, CY). Although the histology of deinopid glands is unknown, one may predict the following peculiarities: 5-10 pairs of major ampullate glands, numerous cylindrical glands, and a single pair of pseudoflagelliform glands.

As a final example of spigot identification, the PMS of *Araneus* have three kinds of spigots: one kind of multiples and two kinds of singulars. The multiple spigots (Fig. 12; AC) are recognizably more like the multiple spigots of the PLS (Fig. 13; AC) than they are like the multiple kind on the ALS (Fig. 11; PI). Probably they are aciniforms. Histological data (Kovoor 1972) suggests that only one sort of gland present in numerous copies exits on both the PMS and PLS: the aciniform glands (#2, above). In this case histology and morphology are again concordant. Similarly, the single posterior spigot on the PMS (Fig. 12; mAP) is more like the single ALS spigot (Fig. 11; MAP), than it is like any single spigot on the PLS. The single anterior spigot on the PMS is more like the two basal spigots on the PLS than it is like other PLS or ALS spigots. Histological data confirms that Araneoidea have a single cylindrical spigot on the PMS and two on the PLS, and only a single minor ampullate gland on the PMS.

Interpretation of patterns.—Once over the hurdle of identifying spigots, one can look for interesting differences among taxa. For example, deinopoid piriform spigots have raised bases with rounded shoulders (Figs. 3, 7; PI), but araneoid piriform spigots have sunken bases and sharp rims. I have found that deinopoids resemble other cribellate araneomorphs, and thus the deinopoid condition is primitive, and the araneoid condition is derived, probably a synapomorphy for the superfamily.

Aciniform spigots usually are small, have longer bases, distinct rims at the base-shaft junction, and elongate, slow-tapering shafts with a fine tip. The PLS aciniform field in *Leucauge* is obviously modified by being narrowed and focused into more regular, elongate rows. I have found the same feature in *Tetragnatha*, *Pachygnatha*, and to a lesser extent in *Meta*, all "metine" genera. It also occurs in at least some linyphiids (e.g., *Frontinella*, Fig. 41). Perhaps it is a synapomorphy for the same group of derived araneoids defined by use of an inside first leg forward tap during sticky segment localization behavior (Coddington 1986a). The distribution of PMS aciniform spigots is also intriguing. In *Araneus*, *Mecynogea*, and *Cyrtophora* a brush of aciniform spigots on the anterior face of the PMS is present (Figs. 12, 16, 20; AC). In the same position, cribellate orbweavers such as *Deinopis* and *Octonoba* (Figs. 4, 8) have paracribellar spigots, but they also have an extensive anterior brush of aciniform spigots. This is also true, for example, of *Micrathena* and *Cyclosa* among the araneids, various other deinopids and uloborids, and potential cribellate outgroups to orbweavers such as amaurobiids. An extensive anterior PMS aciniform brush is probably a plesiomorphic feature. More derived araneoids, such as *Leucauge*, *Latrodectus*, *Theridula*, *Gaucelmus*, and *Frontinella* illustrated here, have no similar anterior aciniform brush. *Nephila* also lacks aciniform spigots in the same area (Kovoor 1986; pers. obs.). The trait is also present in Anapidae, Theridiosomatidae, Mysmenidae, and other theridiids, nesticids, tetragnathids and linyphiids not illustrated here. Perhaps it is

related to increasing specialization of the spinning apparatus. Kovoov and Peters (1988) noted that histologically two classes of aciniform glands exist, aciniform A and aciniform B. I find that distinguishing their spigots with SEM is difficult, but, based on the uloborid *Polenecia*, they suggested that aciniform B spigots were somewhat larger. Interestingly, they also point out that linyphiids, metines, and theridiids (at least) among the araneoids lack aciniform A glands. Very possibly the reduced PMS aciniform field which can be seen with the SEM is the external morphological evidence for the lack of aciniform A glands among derived araneoids. If so, a reduced complement of PMS glands and spigots becomes an additional synapomorphy of derived araneoids (see Coddington 1986a for others), and is the first evidence for a more exact placement of theridiid-necticids among the araneoids.

The reduction and focusing of aciniform spigots on both the PMS and PLS in derived araneoids correlates well with the absence (or reduction) of prey-wrapping behavior. Aciniform spigots probably are mostly responsible for the threads used in prey-wrapping (Table 1). As intimated previously (Coddington 1986a), prey-wrapping and in particular attack-wrapping seems to be a plesiomorphic feature of orbweavers that has been lost in the more derived lineages. This interpretation, which follows directly from cladistic reasoning and outgroup comparison, contradicts previous hypotheses about the evolutionary history of prey-wrapping that were based on the assumed adaptive value of the trait (Robinson 1975; Eberhard 1982). It also illustrates how adaptive hypotheses formed in the absence of cladistic information can mislead (Coddington 1988).

Some patterns are harder to explain. For example, *Araneus*, *Mecynogea*, *Cyrtophora*, *Leucauge*, and *Gaucelmus* all have what appears to be a vestigial spigot on the PMS, posterior to the mAP spigot (Figs. 12, 16, 20, 24, 36). It is probably the vestigial remnant of a minor ampullate gland spigot which is lost in the adult instar (like the vestigial ALS major ampullate, e.g., Figs. 1, 15). This nubbin is absent in *Theridula*, *Latrodectus*, *Frontinella*, and the cribellates. With this distribution, the feature might be another araneoid synapomorphy, uniquely lost in theridiids, or a synapomorphy of theridiids plus linyphiids, but one would need more evidence to say.

The data presented here also bear on a question in the spinneret histology literature. Based on histological evidence, Kovoov (1977c, 1978) was unsure whether the uloborid pseudoflagelliform gland was homologous to the araneoid flagelliform gland. They are apparently similar in shape, anatomy, and chemistry. Micrographs show that orb weavers all have a distinctive PLS spigot on the anterior margin. The morphology and placement of the spigot strongly suggest an interpretation of homology.

Nevertheless, Kovoov and Peters (1988) recently denied homology between flagelliform and pseudoflagelliform glands (and presumably their spigots), and also the monophyly of orbweavers. However, their arguments, when closely analyzed, misconstrue accepted rules of phylogenetic inference. They assert only that araneoids possess features not found in Deinopoidea (aggregate glands—an autapomorphy of Araneoidea); that Deinopoidea possess some features not found in araneoids (the cribellum, calamistrum, and paracribellum—plesiomorphies found in many cribellate taxa); and they imply that the pseudoflagelliform and flagelliform glands and spigots “cannot be regarded as homologous.” The first two assertions are irrelevant to the problem at hand because they refer to an

autapomorphy and a plesiomorphy, respectively, and they unfortunately do not detail their evidence for the last assertion. On the other hand, they admit the many behavioral and web-architectural similarities between cribellate and ecribellate orbweavers, and presumably acknowledge the additional morphological similarities (Coddington 1986a). Given this suggestion of monophyly, and the lack of any evidence that links deinopoids or araneoids to a non-orbweaving group, most phylogeneticists would accept Hennig's principle that features should be regarded as homologues unless contradictory evidence overrules that inference. Put another way, one accepts the homology of bird wings and mammal forelimbs not because the differences between the structures are small or large, but because we have no evidence to contest the inclusion of birds and mammals in tetrapod amniotes. Exactly the same situation obtains in the case of the Orbiculariae (= Deinopoidea plus Araneoidea).

If both spigot morphology and gland histology agree, as in the issues of identification discussed above, then homology statements are doubly strong. If one source of evidence is suggestive but ambiguous, the other may resolve the issue, as for pseudoflagelliform and flagelliform glands. If actual conflicts in synapomorphy schemes exist, however, it would be difficult to decide with complete objectivity which source to accept, especially since we do not have much experience in evaluating for phylogeny either gross spigot morphology, or histochemistry and gland ultrastructure.

Comparison with histological and behavioral data.—It is interesting that a surprisingly high number of histochemical and ultrastructural facts have not been concordant with other comparative data on spiders, and thus with inferred phylogenies. Some strange examples are: an S-shaped major ampullate gland is characteristic of Hersiliidae and Nephilinae (Kovoor 1987); the proximal part of the ampullate gland is reduced to a collar of cells in, e.g., *Hypochilus*, *Filistata*, *Dictyna*, *Amaurobius*, *Telema*, *Pholcus*, *Uroctea*, and *Linyphia* (but not in *Oecobius* or other araneoids); three secretory regions are only present in the ampullate glands of *Cyrtophora*, *Cyclosa*, and *Gasteracantha* (not a monophyletic group), but only two in remaining araneids; pyriform glands are tripartite in *Leucauge* and *Oecobius*, but unipartite in *Uroctea* and, presumably, other metines; *Hersilia*, but not *Oecobius* or *Uroctea*, has tripartite aciniform glands; amino terminal groups are present in aciniform glands of theridiids and linyphiids, which apparently correspond to the aciniform B glands of Araneidae, Hersiliidae, and *Polenecia* uniquely among the uloborids (most examples from summary in Kovoor 1987). Any biologist familiar with corroborated phylogenies of spiders would be puzzled, to say the least, by the above groupings.

I am not sure why this is so. It may be because histochemical analysis often focuses on the chemical *behavior* of molecules, and not on their informational structure. The same lack of concordance with other systematic information was apparent in the early biochemical analysis of enzymes that gave, for example, percentages of specific amino acids, pH data, or molecular weights. Only later did biochemists discover that the informational content of enzymes was in the sequence of amino acids, rather than their relative abundances or other such summary features. Likewise, chemical characterizations of glandular products, for example as "acidophilic", "tyrosine-rich", "carboxyl-rich", or "rich in reducing groups" simply may not identify conservative phylogenetic features. While realizing that the phylogenetic analysis of these ultrastructural characters is still

young, at this point it is clear that observed points of similarity in some cases contradict massively corroborated phylogenetic groupings. Therefore homology arguments based on histochemistry and ultrastructure apparently need careful evaluation.

Whether the same difficulties of interpretation will characterize the study of gross morphology and distribution of spigots remains to be seen. Thus far the best known groups are the araneoids, and their spigot distributions are apparently more or less concordant with other phylogenetically useful character systems.

Spinning behavior obviously must depend to some extent on spinnerets and spigots. Therefore it is appropriate to comment also on recent behavioral research. Eberhard (1987) recently studied aspects of cribellate web-building behavior in what are apparently primitively non-orbweaving groups. He concluded that the tendency to spin sticky silk centripetally in cribellate and ecribellate orbweavers was widespread and probably plesiomorphic. That is, other non-orbweaving cribellate taxa such as filistatids, eresids, psechrids, and dictynids also start the spinning of sticky silk at the edge of their webs, and finish at the center or at the retreat. A centripetal tendency in the spinning of cribellate silk outside the true orbweavers was one specific prediction of the monophyly hypothesis (Coddington 1986a: 362). The fact that it occurs in the entire range of cribellate taxa is disappointing because so broad a distribution offers no evidence as to which of these taxa is the sister group of orbweavers. On the other hand, it partially overlaps the distribution of the pseudoflagelliform and paracribellar spigots, and thus all of these features when analyzed in tandem may elucidate araneomorph phylogeny.

In contrast, Eberhard (1987) argued that this widespread behavioral trait made it more plausible that behaviors characteristic of orb-weaving had evolved at least twice. In contrast, I still see no evidence that these behaviors are convergent. As pointed out above, such a conclusion would be logical only if synapomorphic features were discovered that linked only a portion of the orbweavers with a primitively non-orbweaving group.

Of course orbweavers, whether cribellate or not, still exhibit many unique and detailed behaviors, such as laying sticky silk in a continuous spiral, shifting combing legs (cribellates) or plucking-snubbing legs (araneoids) halfway through construction of a single sticky segment, sticky spiral localization, frame behavior, exploration behavior, non-sticky spiral construction, and the over-all algorithm of web construction. Orbweavers are also distinctive among all other major groups of spiders because complete and typical webs are produced in a single behavioral bout, usually lasting a few hours or less. Other web-spinning spiders typically take several days, and several bouts of behavior, to complete the architecture typical of their taxon. The behaviors unique to orbweavers are similar not only in gross aspect and function, but also in the details of movements of individual legs. Many of these appear to be true behavioral synapomorphies for orbweavers. The tendency to lay sticky silk centripetally is all very well, and it may even define a monophyletic group (however huge, if it includes everything from Filistatidae to Araneoidea). Indeed it seems possible that the centripetal tendency in sticky silk spinning may even be a primitive trait of Araneomorphae.

Interestingly, the same sort of conclusion apply to the pseudoflagelliform gland. Kooor (1987) mentions glands "identified as pseudoflagelliform" for eresids, amaurobiids, psechrids, and zoropsid spiders. She also mentions that such glands

are not found in Filistatidae or, surprisingly, in Dictynidae. Histological observations on Hypochilidae, and Austrochilidae have not been published, but I have found several distinctly shaped spigots on the PLS of filistatids, hypochilids, and austrochilids, as well as amaurobiids and eresids. Given the position of flagelliform gland spigots in araneoids and pseudoflagelliform spigots among deinopoids, one would expect to find homologues of these glands uniquely on the PLS. On the other hand, I have not yet found any specialized morphologies in eresids or amaurobiids, and thus something of a contradiction is developing between histological and morphological pattern. Regardless of how this smaller controversy is resolved, if the histological research accurately identifies homologues of the uloborid pseudoflagelliform gland, we may have to conclude that primitive pseudoflagelliform glands and spigots evolved soon after the origin of araneomorph spiders—at least soon after the origin of the Araneoclada (all araneomorphs exclusive of Hypochilidae, Austrochilidae, and Gradungulidae).

Like a “centripetal tendency” in sticky silk spinning, then, the pseudoflagelliform gland would become part of the primitive ground plan for most true spiders. Arguments for the unique homology of the deinopoid and araneoid condition would then depend on further special similarities such as that the single pair of glands opens only on the PLS, and that they provide the sole pair of base fibers of the sticky line in both cases.

Conclusions.—Taken together, the spigot evidence thus far corroborates the hypothesis of orbweaver monophyly, and certainly does not dispute it. The spinning fields of cribellate orbweavers are more similar to those of ecribellate orbweavers than they are to non-orbweaving cribellate groups. Among araneoids, the Araneidae still exhibit fairly primitive spinneret morphologies. The same can be said for the details of web construction (Coddington 1986a, b). As always, being primitive in one feature does not make a taxon primitive in all respects. Thus araneid genitalia may be relatively more derived than those of metines or the symphytognathoid taxa, or at least far from the orbweaver ground plan.

All of the spiders considered here are orbweavers, or are descended from orbweavers, based on other evidence. Although this character system is obviously useful within the orbweavers, it would be interesting to know how well this system of logic will work for more distantly related, and less derived cribellate groups which may be the sister taxon to orbweavers, such as Hypochiloidea, Amaurobioidea, or Dictynoidea. Even though among distantly related and little studied groups the use of the conventional names for araneoid glands becomes increasingly risky and less justifiable, the basic method of comparing between singulars and multiples, between sexes and instars, and from one spinneret to another should be a primary tool for deciphering spigot homology.

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is to Jacqueline Kovoov, whose steady investigation of spider spinning structures first suggested this study, and provided the context that made it possible.

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FOLIAGE-DWELLING SPIDERS IN THREE CENTRAL FLORIDA PLANT COMMUNITIES

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ABSTRACT

Foliage-dwelling spiders were collected using sweep nets in pond pine, sand pine scrub, and flatwoods plant communities on the University of Central Florida campus near Orlando. Collections were made bimonthly from May, 1983 through March, 1984.

A total of 4,022 spiders was collected; 2,076 in pond pine, 1,258 in sand pine scrub, and 688 in flatwoods. Spider diversity was greatest in pond pine, followed by sand pine scrub and then flatwoods community. Similarity in spider species was greatest between pond pine and flatwoods.

Salticids represented 40.2% of the combined populations. *Misumenops celer* (Hentz) was found in all three plant communities and was abundant.

INTRODUCTION

The southeastern United States has a rich spider fauna. Investigators have studied the spider fauna in North Carolina (Barnes 1953; Barnes and Barnes 1955; Berry 1970, 1977). In Florida, Muma (1973), Rey and McCoy (1983), and Lowrie (1963, 1971) have sampled the spider fauna.

The foliage-dwelling spiders of the pond pine, sand pine scrub, and flatwoods communities have not been described. The scorpion, pseudoscorpion, opilionid, and ground surface spider faunas in these communities have been described (Corey and Taylor 1987).

This paper compares the foliage-dwelling spider faunas in the pond pine, sand pine scrub, and flatwoods communities. In addition we show seasonal differences in the three communities.

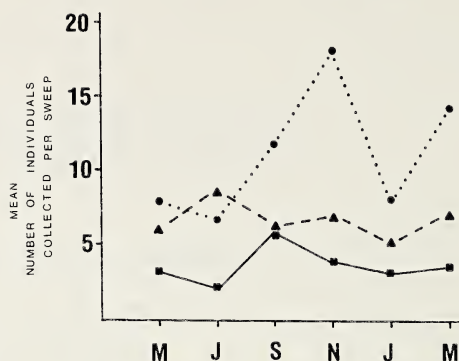
MATERIALS AND METHODS

Study sites.—The three plant communities where our study occurred lie in the eastern part of the University of Central Florida campus, located approximately 17 km east of Orlando in Orange County (S10 R31E T22S). The three plant communities studied were pond pine, sand pine scrub and flatwoods. For a description of the plant communities, see Corey (1987) and Corey and Taylor (1987).

Methods.—The sweep net consisted of a 91.4-cm handle, 40.6-cm ring, and collecting bag made of white canvas. A single sweep consisted of; 1) first stroke

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Figure 1.—Mean number of spiders caught on foliage using sweep nets in pond pine (●), sand pine scrub (▲), and flatwoods (■).



of the net started on the left and moved toward the right forming a 180 degree arc, 2) the second stroke covered the same area as the first stroke, but the net was moved in the opposite direction, 3) after completing the two strokes, one step forward was taken and the two-stroke method was repeated (for 100 steps), 4) then the 100 steps were retraced using the two-stroke method. Each sweep consisted of 1,200 strokes.

Thirty sets of sweeps per collecting month per plant community were made beginning in May 1983 and ending in March 1984 for a total of 540 sweeps. Sweeps were made on three consecutive days, one day for each community. All materials netted were placed into plastic bags and returned to the laboratory. Spiders were separated from the debris and placed into baby food jars containing 70% ethanol.

Identification.—Spiders were identified using a dissecting microscope. Difficult specimens were identified or verified by Jonathan Reiskind, University of Florida; James H. Redner, Biosystematics Research Institute; Norman I. Platnick, American Museum of Natural History; G. B. Edwards, Florida State Collection of Arthropods; and Jonathan Coddington, Smithsonian Institution.

All spiders were identified to lowest possible taxon. Many immatures were identified only to family level. Some spiders collected in poor condition could not be identified to family; these specimens are reported as undetermined (See Table 3).

RESULTS AND DISCUSSION

Four-thousand and twenty-two spiders from 18 families and 89 species were collected using sweep nets; 2,076 individuals, 14 families and 58 species from pond pine, 1,258 individuals, 15 families and 53 species from sand pine scrub, and 688 individuals, 13 families and 54 species from flatwoods. See appendix for a complete list of the spider species. An average of 7.45 spiders per sweep was observed. Figure 1 shows the mean number of individuals collected per sweep for the six collecting periods. Sixty-nine percent more spiders were found in pond pine than in flatwoods, 39% more in pond pine than in sand pine scrub, and 45% more in sand pine scrub than in flatwoods.

Analysis of guild composition shows differences between communities (Fig. 2). Guilds were patterned after Gertsch (1979). Guilds are (1) jumping spiders; Salticidae, (2) crab spiders; Thomisidae and Philodromidae, (3) aerial web spinners; Theridiidae, Linyphiidae, and Araneidae, (4) hunting spiders; Pisauri-

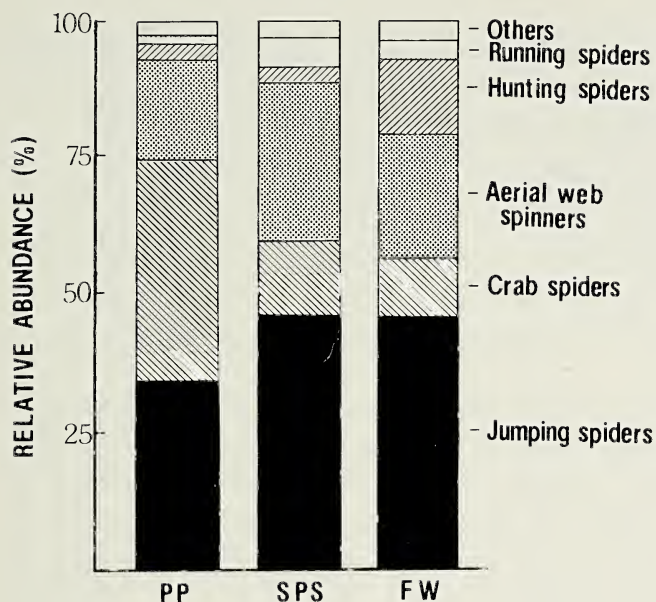


Figure 2.—Guild composition of individual spiders for the three study sites. PP = pond pine, SPS = sand pine scrub, and FW = flatwoods.

dae, Lycosidae, and Oxyopidae, (5) running spiders; Gnaphosidae, Clubionidae, and Anyphaenidae, and (6) others; remainder of the spiders. Relative abundance of jumping spiders declined in pond pine compared to that of sand pine scrub and flatwoods. Crab spiders increased substantially in pond pine.

Simpson's Index of Diversity was calculated for the three communities (Simpson 1949). Pond pine had a value of 0.84, sand pine scrub of 0.88, and flatwoods of 0.89. These low values may be due to the high species richness found in each community and the small number of dominant species.

Sorensen's Index of Similarity (Krebs 1978) was used to determine the similarities of spider species composition among communities. Species composition was more similar between pond pine and flatwoods (0.68), followed by sand pine scrub and flatwoods (0.63). Pond pine and sand pine scrub (0.57) were least similar. It was expected that habitats with similar vertical plant structure would be similar in spider species. This relationship, however, was not true; pond pine was less similar to sand pine scrub than to flatwoods as to species composition. Height and vertical structure of the vegetation swept may have allowed a greater spider abundance, but not a greater similarity in species. Pond pine had the highest understory swept (3 m) and the largest number of spiders, followed by sand pine scrub (averaged 2 m). Flatwoods with a low understory (averaged 1.5 m) had the smallest number of spiders.

Pond pine community had the most complex vegetation layer and this may have attributed to its having a greater spider abundance. Few herbaceous plants occurred in flatwoods as compared to pond pine and sand pine scrub. Flatwoods had a smaller surface area for spiders and this may account for the low abundance.

Table 1 shows the mean number of individual spiders occurring in the three communities. For each monthly mean, 95% confidence intervals were calculated as $\bar{x} + t$ (SE) (Simpson et al. 1960). Pond pine in November was significantly different from the other communities in mean number of spider individuals.

Table 1.—Mean number of individual spiders occurring on foliage in the study sites by collection month.

Collection month	Community		
	Pond pine $\bar{x} \pm (SE)$	Sand pine scrub $\bar{x} \pm (SE)$	Flatwoods $\bar{x} \pm (SE)$
May	81.33 (13.40)	64.33 (2.89)	34.33 (1.77)
July	70.67 (9.85)	90.00 (5.69)	26.00 (4.59)
September	123.33 (26.97)	66.00 (4.01)	10.41 (6.02)
November	186.00 (5.04)	73.00 (11.15)	10.26 (5.93)
January	81.67 (19.17)	53.33 (10.94)	8.14 (4.71)
March	147.67 (29.79)	98.33 (26.69)	8.14 (4.71)

Mean numbers of individuals captured in flatwoods in May, July, and September were less than and significantly different from sand pine scrub, but not from pond pine, which had large standard errors associated with the means. In contrast, mean number of spider species captured in flatwoods in July were significantly different ($p = 0.05$) from the other two communities (Table 2). Pond pine in November was significantly different from flatwoods in mean number of species. The lack of significant differences may be due to the large variance in number of individuals and species found among the communities.

Spider families, represented by individuals collected on foliage, are listed in Table 3. The three most common families for all communities were salticids, thomisids, and linyphiids; these represent 76.5% of all spiders captured in sweeps. In pond pine, thomisids, salticids, and linyphiids represented 82.4% of that community's total spider assemblage. In sand pine scrub, salticids, linyphiids, and thomisids represented 74.8% of the total spider assemblage. In flatwoods, salticids, oxyopids, and araneids represented 71.6% of the total spider assemblage. Figure 3 shows seasonal abundance of three common families occurring on foliage.

Table 4 shows the 10 most common species collected by frequency of occurrence. Abundant species were *Thiodina sylvana* (Hentz) and *Misumenops celer* (Hentz).

Twenty-seven species occurred in all communities (Table 5). No single species was common in all three communities. Nine species of spiders were collected from only one of the three communities: *Uloborus glomosus* (Walck.), *Pholcomma hirsutum* Emerton, *Neriene radiata* (Walck.), *Ceratinopsis* sp., *Tibellus oblongus* (Walck.) and *Zygoballus rufipes* (Peckham & Peckham) in pond pine; *Hyptiotes*

Table 2.—Mean number of spider species occurring on foliage in the study sites by collection month.

Collection month	Community		
	Pond pine $\bar{x} \pm (SE)$	Sand pine scrub $\bar{x} \pm (SE)$	Flatwoods $\bar{x} \pm (SE)$
May	17.33 (0.88)	16.00 (3.61)	12.33 (1.46)
July	14.33 (0.88)	17.33 (1.46)	8.00 (0.58)
September	13.67 (1.46)	11.00 (0.58)	13.33 (2.89)
November	18.33 (0.88)	15.33 (1.77)	12.00 (0.58)
January	10.67 (0.34)	11.67 (0.88)	8.33 (0.88)
March	17.67 (1.86)	15.67 (1.77)	13.00 (1.53)

Table 3.—Number of individuals and percent of spiders by family for the three communities collected with sweep nets.

	Pond pine		Sand pine		Flatwoods		Total	
	#	%	#	%	#	%	#	%
Uloboridae	6	0.3	5	0.4	0	0.0	11	0.3
Dinopidae	1	0.1	0	0.0	0	0.0	1	0.02
Dictynidae	0	0.0	1	0.1	0	0.0	1	0.02
Theridiidae	95	4.6	52	4.1	20	2.9	167	4.2
Linyphiidae	168	8.1	206	16.4	35	5.1	409	10.2
Linyphiinae	93	4.5	6	0.5	20	2.9	119	3.0
Erigoninae	75	3.6	200	15.9	15	2.2	290	7.2
Araneidae	115	5.5	101	8.0	79	11.5	295	7.3
Tetragnathidae	10	0.5	2	0.2	16	2.3	28	0.7
Agelenidae	0	0.0	0	0.0	7	1.0	7	0.2
Hahniidae	0	0.0	4	0.3	0	0.0	4	0.1
Pisauridae	0	0.0	0	0.0	2	0.3	2	0.05
Lycosidae	3	0.1	1	0.1	0	0.0	4	0.1
Oxyopidae	27	1.3	43	3.4	92	13.4	162	4.0
Gnaphosidae	3	0.1	1	0.1	3	0.4	7	0.2
Clubionidae	35	1.7	30	2.4	6	0.9	71	1.8
Anyphaenidae	19	0.9	34	2.7	11	1.6	64	1.6
Thomisidae	836	40.3	146	11.6	66	9.6	1048	26.1
Philodromidae	9	0.4	3	0.2	3	0.4	15	0.4
Salticidae	706	34.0	589	46.8	321	46.7	1616	40.2
Undetermined	43	2.1	40	3.2	27	3.9	110	2.7

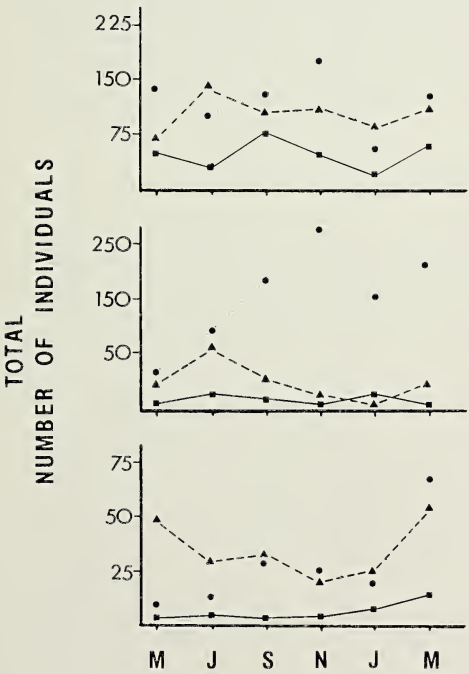


Figure 3.—Seasonal distribution of the most common families of foliage-dwelling spiders caught with sweep nets in pond pine (●), sand pine scrub (▲), and flatwoods (■). Salticidae (upper), Thomisidae (middle), and Linyphiidae (lower).

Table 4.—Ten most common spider species ranked by frequency of occurrence within each plant community. NR = no rank assigned.

Species	Pond pine	Sand pine scrub	Flatwoods
<i>Synema viridans</i>	1	NR	9
<i>Thiodina sylvana</i>	2	5	5
<i>Misumenops celer</i>	3	4	3
<i>Lyssomanes viridis</i>	4	3	NR
<i>Frontinella pyramitela</i>	5	NR	8
<i>Theridula</i> sp.	6	NR	NR
<i>Hentzia palmarum</i>	7	1	1
<i>Phidippus pulcherrimus</i>	7	NR	NR
<i>Grammonota</i> sp. #1	9	2	NR
<i>Leucage venusta</i>	10	NR	NR
<i>Grammonota</i> sp. #2	NR	6	NR
<i>Hypsosinga pygmaea</i>	NR	7	NR
<i>Aysha gracilis</i>	NR	8	NR
<i>Marpissa pikei</i>	NR	9	4
<i>Tmarus floridensis</i>	NR	10	NR
<i>Peucetia viridans</i>	NR	NR	2
<i>Phidippus</i> sp.	NR	NR	6
<i>Acacesia hamata</i>	NR	NR	7
<i>Oxyopes salticus</i>	NR	NR	9

Table 5.—Spiders occurring in all three plant communities. R = rare (less than 1% of total population for that community), P = present (1% to 4.9% of total population), and C = common (5% or more of the total population).

Species	Pond pine	Sand pine scrub	Flatwoods
<i>Theridula</i> sp.	P	P	R
<i>Thymoites unimaculatum</i>	R	P	R
<i>Frontinella pyramitela</i>	P	R	P
<i>Grammonota</i> sp. #1	P	C	P
<i>Leucauge venusta</i>	P	R	R
<i>Argiope aurantia</i>	R	R	P
<i>Acacesia hamata</i>	R	P	P
<i>Neoscona domiciliorum</i>	R	R	R
<i>Hypsosinga pygmaea</i>	R	P	R
<i>Wagneriana tauricornis</i>	R	R	R
<i>Peucetia viridans</i>	R	P	C
<i>Oxyopes salticus</i>	R	R	P
<i>Aysha gracilis</i>	R	P	P
<i>A. velox</i>	R	R	R
<i>Tmarus floridensis</i>	R	P	R
<i>Misumenops celer</i>	C	C	P
<i>Synema viridans</i>	C	R	P
<i>Paramaevia michelsoni</i>	R	R	R
<i>Marpissa pikei</i>	R	P	P
<i>Hentzia palmarum</i>	P	C	C
<i>Zygoballus rufipes</i>	R	R	R
<i>Thiodina sylvana</i>	C	P	P
<i>Lyssomanes viridis</i>	C	C	R
<i>Phidippus</i> sp.	R	R	P
<i>Phidippus pulcherrimus</i>	P	R	R

cavatus (Walck.) in sand pine scrub; and *Agelenopsis naevia* (Walck.) and *Coriarachne* sp. in flatwoods.

Peucetia viridans (Hentz) and *Lyssomanes viridis* (Walck.) overwintered as juveniles. Berry (1971) found several spider species to overwinter as juveniles in the North Carolina Piedmont. He also found that adults and juveniles of some species appeared in large numbers at the same time of the year after a period of time when no or very few adults and juveniles were found. The following spiders exhibited this behavior in our study: *Grammonota* sp. #1 and *Misumenops celer* in pond pine, *Thymoites unimaculatum* (Emerton) and *Hypsosinqua pygmaea* (Sundevall) in sand pine scrub, and *Hentzia palmarum* (Hentz) in flatwoods. This behavior may be a result of rapid maturation.

Lowrie (1963, 1971) studied oxyopids in the vegetation strata in northern Florida. Of five species he collected, *Oxyopes salticus* (Hentz) and *Peucetia viridans* were represented in our study.

Rey and McCoy (1983) studied arachnids for fifteen months in tidal marshes of northwest Florida and collected 47 species and 14 families. The following eight species were represented in their study and in our study: *Nephila clavipes* (L.), *Oxyopes salticus*, *Peucetia viridans*, *Tetragnatha laboriosa* Hentz, *Florinda coccinea* (Hentz), *Metaphidippus galathea* (Walck.), *Marpissa pikei* (G. & E. Peckham), and *Synemosyna petrunkevitchi* (Chapin).

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APPENDIX

SPIDERS IN THREE CENTRAL FLORIDA PLANT COMMUNITIES

Species of spiders collected with sweep nets are listed by family and community: Pond pine (PP), sand pine scrub (SPS), and flatwoods (FW).

Family	Species	PP	SPS	FW
Dinopidae	1. <i>Dinopis spinosa</i> Marx	1		
TOTALS		1	0	0
Uloboridae	2. <i>Uloborus glomus</i> (Walck.)	6		
	3. <i>Hyptiotes cavatus</i> (Hentz)		5	
TOTALS		6	5	0
Dictynidae	4. <i>Dictyna</i> sp.		1	
TOTALS		0	1	0
Theridiidae		13	17	9
	5. <i>Pholcomma hirsutum</i> Emerton	7		
	6. <i>Spintharus flavidus</i> Hentz	1		1
	7. <i>Theridula</i> sp.	66	17	4
	8. <i>T. unimaculatus</i> (Emerton)	2	17	3
	9. <i>Theridion flavonotatum</i> Becker	1		2
	10. <i>Steatoda triangulosa</i> (Walck.)	1	1	
	11. <i>Stemmops bicolor</i> (OPC)	1		
	12. <i>Argyrodes elevatus</i> (Walck.)	3		1
TOTALS		95	52	20
Linyphiidae				
Linyphiinae		3	3	1
	13. <i>Frontinella pyramitela</i> (Hentz)	68	3	14
	14. <i>Neriere radiata</i> (Walck.)	7		
	15. <i>Florinda coccinea</i> (Hentz)	15		5
Totals		93	6	20
Erigoninae		16	16	5
	16. <i>Grammonota</i> sp. #1	48	142	7
	17. <i>Grammonota</i> sp. #2	3	36	
	18. <i>Grammonota</i> sp. #3		4	
	19. <i>Ceratinopsis</i> sp.	6		
	20. Species #1	1		
	21. Species #2	1		
	22. Species #3		2	3
TOTALS		75	200	15

Araneidae	17	10	25
23. <i>Gasteracantha elipsoides</i> (Walck.)	1		
24. <i>Micrathena gracilis</i> (Walck.)	1	2	
25. <i>M. sagittata</i> (Walck.)	1		
26. <i>Leucauge venusta</i> (Walck.)	43	4	2
27. <i>Nephila clavipes</i> (Linnaeus)	1		
28. <i>Argiope</i> sp.			1
29. <i>A. aurantia</i> Lucas	5	12	8
30. <i>Mangora placida</i> (Hentz)	9		6
31. <i>Acanthepeira stellata</i> (Marx)	2		10
32. <i>Acacesia hamata</i> (Hentz)	6	24	15
33. <i>Neoscona arabesca</i> (Walck.)			1
34. <i>N. domiciliorum</i> (Hentz)	3	1	1
35. <i>Araneus minatus</i> (Walck.)	1	1	
36. <i>Hyposinga rubens</i> (Hentz)		13	1
37. <i>H. pygmaea</i> (Sundevall)	1	28	3
38. <i>Wagneriana tauricornis</i> (OPC)	15	5	1
39. <i>Scoloderis cordatus</i> (Tacz.)		1	1
40. Species #1	9		4
TOTALS	115	101	79
Tetragnathidae	7	1	8
41. <i>Tetragnatha</i> sp.	2		3
42. <i>T. laboriosa</i> Hentz	1		2
43. <i>T. straminea</i> Emerton		1	3
TOTALS	10	2	16
Agelenidae			2
44. <i>Agelenopsis naevia</i> (Walck.)			5
TOTALS	0	0	7
Hahniidae			
45. <i>Hahnia cinerea</i> Emerton		4	
TOTALS	0	4	0
Lycosidae	3	1	0
Pisauridae	0	0	2
Oxyopidae	5	22	35
46. <i>Peucetia viridans</i> (Hentz)	18	15	45
47. <i>Oxyopes salticus</i> (Hentz)	4	6	11
48. <i>Hamataliwa grisea</i> Key.			1
TOTALS	27	43	92
Gnaphosidae	3		3
49. <i>Poecilochroa decorata</i> (Kaston)		1	
TOTALS	3	1	3
Clubionidae	14	25	5
50. <i>Trachelas deceptus</i> (Banks)		1	
51. <i>T. similis</i> (FOP Cambridge)		1	
52. <i>Chiracanthium inclusum</i> (Hentz)	1	2	
53. <i>Clubionoides</i> sp.	20		1
54. <i>C. gertschi</i> Kaston		1	
TOTALS	35	30	6
Anyphaenidae	2		1
55. <i>Aysha gracilis</i> (Hentz)	10	27	7
56. <i>A. velox</i> (Becker)	3	7	3
57. <i>Wulfila alba</i> (Hentz)	4		
TOTALS	19	34	11
Thomisidae	43	28	14
58. <i>Tmarus</i> sp.		4	2
59. <i>T. floridensis</i> Key.	4	25	3
60. <i>Misumenops celer</i> (Hentz)	190	75	26
61. <i>Misumenops asperatus</i> (Hentz)		4	

	62. <i>M. oblongus</i> (Key.)		1	
	63. <i>Misumenoides formosipes</i> (Walck.)	1		4
	64. <i>Synema viridans</i> (Banks)	598	9	11
	65. <i>Coriarachne</i> sp.			5
	66. <i>Xysticus variabilis</i> Key.			1
TOTALS		836	146	66
Philodromidae				
	67. <i>Ebo contrastus</i> (RJS & NIP)	1		
	68. <i>Philodromus placidus</i> Banks		1	
	69. <i>P. rufus</i> Walck.		2	3
	70. <i>P. formosipes</i> (Walck.)	3		
	71. <i>Tibellus oblongus</i> (Walck.)	5		
TOTALS		9	3	3
Salticidae		106	132	106
	72. <i>Synemosyna formica</i> (Hentz)		2	
	73. <i>S. petrunkevitchi</i> (Chapin)			1
	74. <i>Peckhamia picata</i> (Hentz)		3	
	75. <i>Paramaevia michelsoni</i> (Barnes)	4	6	6
	76. <i>Marpissa pikei</i> (G & E Peckham)	11	26	24
	77. <i>Agassa cerulea</i> (Walck.)			1
	78. <i>Hentzia palmarum</i> (Hentz)	52	265	127
	79. <i>Zygoballus rufipes</i> P&P	11	1	1
	80. <i>Z. sexpunctatus</i> (Hentz)		1	2
	81. <i>Thiodina sylvana</i> (Hentz)	299	71	19
	82. <i>T. purpera</i> (Hentz)	1		1
	83. <i>Phidippus audax</i> (Hentz)			3
	84. <i>P. pulcherrimus</i> Key.	52	1	6
	85. <i>Phidippus</i> sp.	13	6	16
	86. <i>Metaphidippus galathea</i> (Walck.)	1	1	
	87. <i>M. tillandsiae</i> Kaston		2	2
	88. <i>Admestine tibialis</i> (CL Koch)		4	
	89. <i>Lyssomanes viridis</i> (Walck.)	156	67	6
TOTAL		706	589	321
Unplaced		43	40	27

RESEARCH NOTES

**SCYTODES POENITENS CHAMBERLIN, NOT PNOEITENS
(ARANEAE, SCYTODIDAE)**

In his descriptions of new species from "the shores and islands of the Gulf of Baja California," Chamberlin (1924) showed a great propensity for scientific names with religious or philosophical meanings. For instance, he used such religious terms as *theologus*, *dogmaticus*, *agnosticus*, *reformans*, *protestans*, *calvanisticus* (sic), *catholicus*, and even *scepticus*, and *redempta*. Names with a philosophical reference are: *positivus*, *rationalis*, *empiricus*, *syntheticus*, *eclecticis*, *pragmaticus*, *realisticus*, *scholastica*, *philosopha*. Sometimes these names were used several times in different genera.

Among these was a new species, *Scytodes poenitens*, correctly spelled, and again misspelled in the same paper. Subsequent cataloguers perpetuated the misspelling (Bonnet 1958: 3988), or produced a new misspelling (Roewer 1942: 330). We correct these errors, and present our reasoning.

Scytodes poenitens Chamberlin

Scytodes poenitens Chamberlin 1924:572 (in a list of species of San Marcos Island).

Scytodes pnoeitens Chamberlin 1924:592 (description of the new species); Bonnet 1958: 3988 (printer's error).

Scytodes pnocitens Roewer 1942:330 (*lapsus calami* or printer's error).

The fact that Chamberlin's 1924 paper has two different spellings is sufficient to justify the correction, since there is in the original publication itself clear evidence of an inadvertant error (International Commission on Zoological Nomenclature 1985: Art. 32c). The form *pnoeitens* of Chamberlin is clearly an error of the printer, who simply got the *n* in the wrong place. Roewer's (1942: 330) *pnocitens* is the result of a further error in which the printer, working from Roewer's handwriting, read the *e* as a *c*.

Chamberlin started with the correct *poenitens* (1924: 272) meaning "penitent", correctly formed as the present participle of the Latin verb *poeniteo*. Subsequent references are all misspelled.

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DO FEMALE *MIAGRAMMOPES ANIMOTUS* (ARANEAE, ULOBORIDAE) SPIN COLOR-COORDINATED EGG SACS?

Like other members of their pantropical genus, *Miagrammopes animotus* Chickering females spin capture webs consisting of only a few threads and monitor them from one of their attachment points (Lubin 1986; Lubin et al. 1978). In this position, the spiders' cylindrical abdomens, long, slender legs, and linear web-monitoring postures (Opell 1987) contribute to their twig-like protective resemblance. Unlike most members of the family Uloboridae that produce stellate or lenticular egg sacs (Opell 1984), *Miagrammopes* females construct cylindrical egg sacs consisting of two columns of eggs wrapped tightly with tubuliform (cylindrical) gland silk (Foelix 1982; Lubin et al. 1978; Opell 1984). The color of both *M. animotus* females and their egg-sac-wrapping silk ranges from light tan to brownish gray to dark, rusty red. During the day, females hang contiguously with their egg sacs, maintaining fourth leg contact with the egg sac and first leg contact with a support to which their web is attached (Fig. 1). This alignment of females with their egg sacs enhances the twig-like appearance of both and may reduce threats to the spiders from visually hunting predators such as lizards, birds, wasps, and other spiders, and to their egg sacs from these predators and egg parasitoids. If a female's proximity to her egg sac serves primarily to permit her to chase away egg parasitoids, the pair's stick-like appearance places her in less jeopardy while she tends her egg sac.

Unless the colors of a female and her egg sac are similar, each would appear more distinct and the crypsis of both would be compromised. This study tests the hypothesis that the colors of *M. animotus* females and their egg sacs are linked by determining if the colors of females and sacs are significantly correlated. It was conducted from 20 February to 10 March, 1987 at the Center for Energy and Environmental Research's El Verde field station, located in the Luquillo National Forest of Puerto Rico.

During day and night field observations, I collected a total of 94 *M. animotus* females and their egg sacs. After accumulating 7-21 female-egg sac pairs, I separated each female from her egg sac and placed them in separate vials with matching numbers. To quantify color, I removed each spider and egg sac from its vial, placed it directly onto the paint chips of a Naturalist's Color Guide (NCG) (Smithe 1975), and recorded the best color match. Specifically, I used the 1981 color dilution series 1 and 2 of sepia and raw umber pigments and series 1 of Vandyke brown pigment. This provided 25 possible colors, 13 of which were matched by females and egg sacs. I scored egg sac and spider color in separate observational series conducted from 1400-1700 under natural light. If the dorsal



Figure 1.—A female *Miagrammopes animotus* (arrow) monitoring her cylindrical egg sac.

surface of a female's abdomen was made noticeably lighter by guanine deposits, I selected the best match of the spider's cephalothorax, legs and lateral abdominal regions.

Each color in the NCG has a Munsell Notation that provides range, value, and chroma indexes. Range has ten categories extending from red through red purple and each category has ten subdivisions. All spiders and egg sacs collected were in the yellow-red and yellow ranges. Value indicates the "darkness" of the color as it would appear in the absence of color vision: black is 0, white is 10. Chroma is an open-ended scale, specifying the intensity of a color's hue. Figure 2 presents the distribution of these three indexes for *M. animotus* females and egg sacs.

Female and egg sac colors are significantly correlated as measured by all three indices: $r = 0.35$ (range), $r = 0.58$ (value), $r = 0.31$ (chroma); $p < 0.003$. Spiders were more reddish yellow than their egg sacs (mean spider range 8.6, SD 1.8; egg sac mean 9.4, SD 1.4), were darker than their egg sacs (mean spider value 4.1, SD 0.7; egg sac mean 5.2, SD 1.1), and had less highly saturated colors than their egg sacs (mean spider chroma 2.7, SD 0.8; egg sac mean 3.2, SD 1.2). Standard errors for spider-egg sac differences were: range 0.2, value 0.1, and chroma 0.1.

Just as background selection enhances the cryptic appearance of insects and spiders (e.g., Malcom and Hanks 1973; Opell 1986; West and Hazel 1979) and protects them from predation (e.g., Erichsen et al. 1980; Sims and Shapiro 1983; West and Hazel 1982), the mechanism linking spider integument and egg sac silk pigmentation probably optimizes the protective resemblance of the pair. The similarity of spider and egg sac color range ("color") should make the pair less conspicuous to predators with color vision, whereas the similarity of color value ("grayness") should make them less conspicuous to predators that lack color vision or to those vertebrates whose vision relies more heavily on rods than color-sensitive cones under the low light conditions of the forest understory (Levine 1985).

Conspicuous guanine deposits were not present in most spiders and seemed to be more common in lighter specimens, where there was little pigmentation to mask them. Because of their mottled nature and dorsal concentration, these

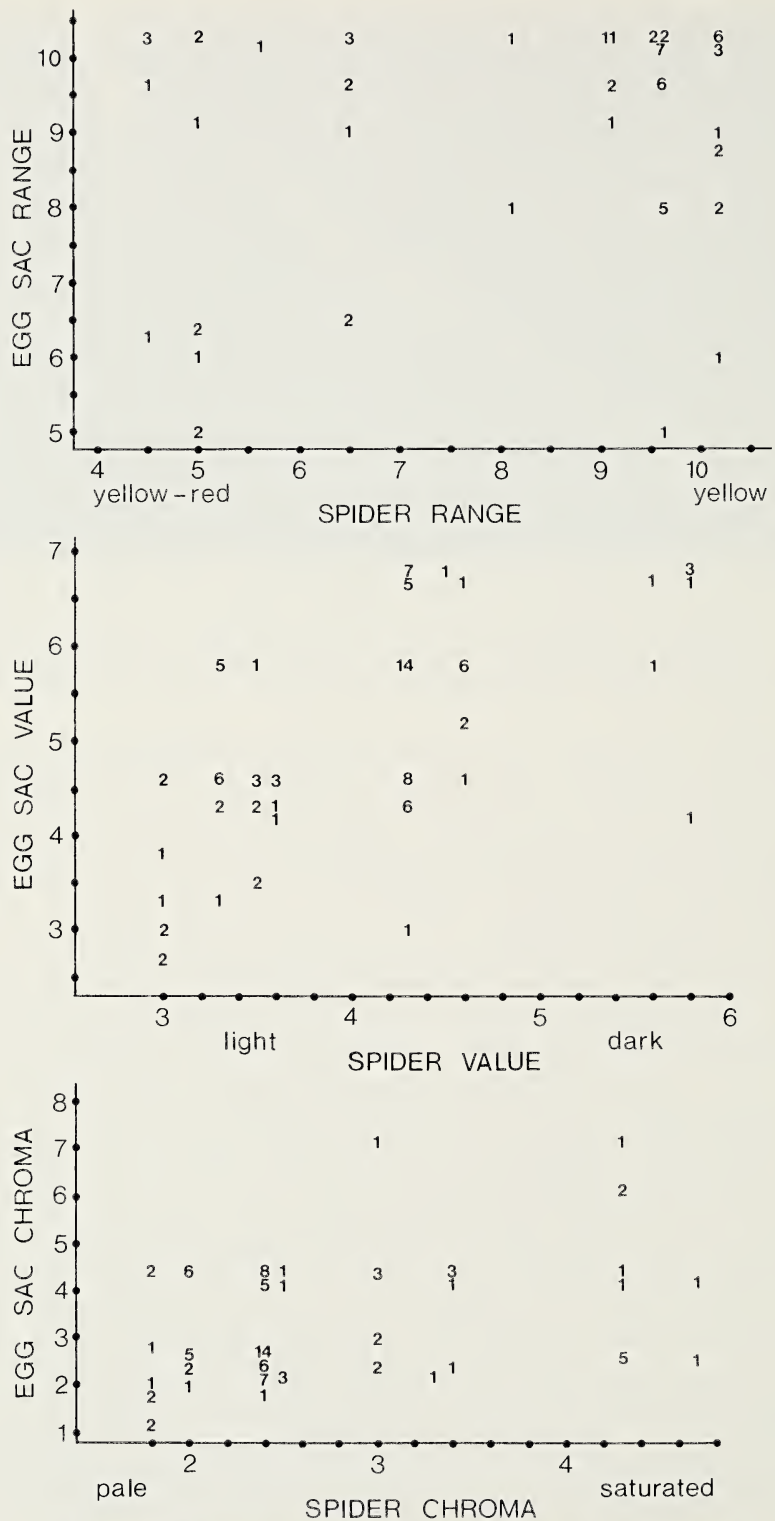


Figure 2. The association between female and egg sac color indexes.

deposits probably do not create significant abdominal color dichotomies that are visible ventrally or laterally.

The color similarity between *M. animotus* females and their egg sacs may be explained either genetically or dietarily, although in spiders there seems to be no clear evidence of the latter (Holl 1986). If metabolized prey pigments are incorporated into both a female's integument and egg sac silk, then feeding history could explain this similarity. If a spider's integumental pigmentation is genetically determined, then these genes may also regulate the color of egg sac silk. During this study I often collected females having greatly different colors from the same bamboo plant or dead palm frond. Although their diets should have been very similar, this observation does not rule out the effects of single, heavily pigmented prey on spider color. However, it does suggest that *M. animotus* do not change their colors to match their backgrounds as do some spiders (see Holl 1986 for a review).

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MEASURING THE STICKINESS OF SPIDER PREY CAPTURE THREADS

Comparative studies of spider orb-web architecture and function make the simplifying assumption that the stickiness of these webs' spiral, prey capture elements is similar. The wide range of spider size, spiral spacing, and web tensions suggests that this may not be true and that capture thread stickiness is an important functional component of web design. Just as the length of capture silk provides an index of material outlay and spiral spacing influences the size of prey captured (Eberhard 1986), silk stickiness determines the web's ability to retain prey until they can be subdued by the spider.

Using a simple balance device, Eisner et al. (1964) compared the retention ability of *Nephila clavipes* (Linn.) viscid thread for naked insect wings with those beset with hairs and scales. However, the stickiness of different species' capture threads have not been compared. To study Uloboridae threads, I designed a simple device for measuring thread stickiness that may be useful to other investigators.

This instrument (Fig. 1) employs a glass needle strain gauge and is similar to the devices used by Craig (1987) for measuring silk tensile strength and Opell (1987) for comparing the web-monitoring forces expressed by spiders. The instrument described here was fabricated from 6 mm thick plexiglass.

Silk samples are collected from a spider's web using a microscope slide, along whose length five 4 mm wide rectangular brass supports are glued at 4 mm intervals. Double-sided tape applied to the top of each support holds the silk under its original tension. This collecting device permits four replicate samples to be taken from each web and the close spacing of its supports minimizes silk extension during the process.

Two clips secure this collecting slide to a sliding platform that permits positioning of each replicate cribellar silk sample under a narrow aluminum contact plate. The latter is glued with epoxy to the tip of a fine glass needle drawn from a hematocrit tube. Thumb screws secure the sliding plate after each sample has been positioned.

The frame holding the calibrated needle can be raised and lowered relative to the microscope slide with a small screw jack. After a small, standard downward force is exerted on the contact plate, the strain gauge is slowly raised until the contact plate attached to the needle's tip pulls free of the capture silk. The position of the needle on the strain gauge's arbitrary scale immediately before the plate pulls free of the thread is noted. When converted to its milligram equivalent using a calibration graph and multiplied by the accelerating force of gravity, this value yields the force in Newtons necessary to overcome the thread's adhesion.

Although the frame is raised by a hand-operated jack, the need to continually observe the glass needle's position on the scale keeps the velocity of silk loading low and fairly constant. In the example given below, scale unit spacing was 632 μm and, in order to record to the nearest half unit the point at which the contact plate pulled free of the silk, the silk was loaded at a velocity of 287-316 μm per second. This velocity is probably less than half that of a struggling prey's appendages. The rate of loading could be more precisely controlled by driving the jack with a small motor, although a greater velocity than that listed above would

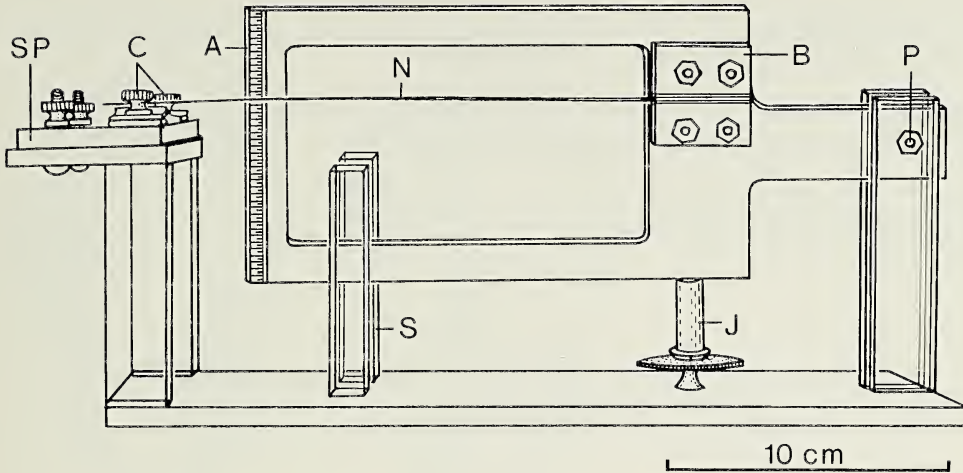


Figure 1.—The instrument used to measure capture silk adhesion. A = arbitrary scale, B = mounting bracket for glass needle, C = clamps for securing microscope slide silk sampler, J = screw jack for raising strain gauge, N = glass needle with contact plate near its free (left) end, P = pivot of strain gauge, S = parallel stabilizing bars to reduce lateral movement of strain gauge, SP = sliding platform for positioning silk samples.

make it difficult to accurately determine visually the point at which the contact plate pulled free of the silk.

To test the reliability of this technique I measured the stickiness of cribellar silk from 21 mature female *Hyptiotes cavatus* (Hentz) webs. All webs were spun in the laboratory and the stickiness of their silk was measured 1-3 days after it was produced. A 2.20 mm wide polished aluminum contact plate was first pressed against each silk sample with a force of 3.03×10^{-5} Newtons. The mean stickiness value of these 84 measurements was 3.251×10^{-5} N / mm of contact (SD = 6.7×10^{-7} N / mm, CV = 2.06). The mean of each web's average stickiness value ($N=21$) had a SD of 4.4×10^{-7} N / mm and a CV = 1.34. Comparative values for the four replicate measurements of each thread ranged from 0 to 5.76 and had a mean of 1.30.

Although cribellar silk leaves no residue on the aluminum contact plate, viscid threads do and the plate must be cleaned with acetone or other solvent before each measurement. A length of dragline thread serves as both a control and a test for a clean contact plate, as the plate should not stick to it.

Gabrielle Roth helped with measurements. John Anderson and Ruth Buskirk provided helpful comments on this paper. This technique was developed during studies supported by NSF grant BSR-8407979 and by a small projects grant from Virginia Tech's College of Arts and Sciences.

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ON A NEW SPIDER OF THE GENUS *DRASSYLLUS* (ARANEAE, GNAPHOSIDAE) FROM FLORIDA

A dozen species of the zelotine gnaphosid genus *Drassyllus* have been reported from Florida (Platnick and Shadab, 1982, *Bull. Amer. Mus. Nat. Hist.*, 173:1-97), among which two, *D. seminolus* Chamberlin and Gertsch and *D. alachua* Platnick and Shadab, appear to be endemic to the state. We report here on an additional species collected from a pine flatwoods plant community in the St. Johns River drainage. We thank the Exline-Frizzell Fund for Arachnological Research of the California Academy of Sciences for supporting the field work that lead to the discovery of this species, and Dr. M. U. Shadab of the American Museum of Natural History (AMNH) for help with the illustrations. The format of the description follows that used in the generic revision.

Drassyllus orlando, new species

Figs. 1-4

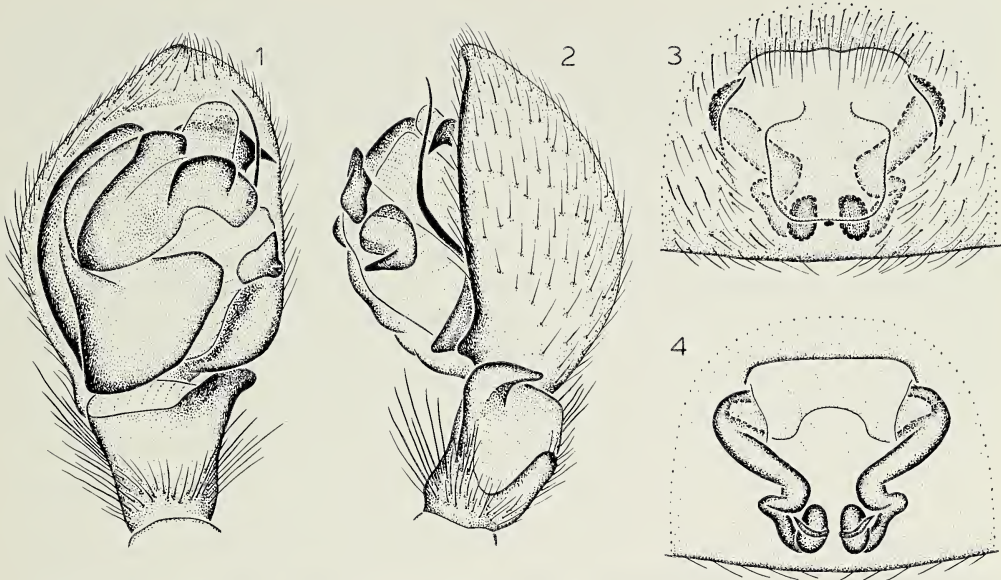
Types.—Male holotype and female allotype taken in a pitfall trap on the University of Central Florida campus, 12 miles east of Orlando, S10 R31E T22S, Orange Co., Florida (25 May 1983; D. T. Corey), deposited in AMNH.

Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—Males can be distinguished from those of all other American *Drassyllus* by the retrolateral depression on the palpal tibia (Fig. 2), females by the widely separated median and anterior epigynal ducts (Fig. 4).

Male.—Total length 3.19-3.58. Carapace 1.43-1.50 long, 1.14-1.20 wide. Femur II 0.94-0.98 long (four specimens). Eye sizes and interdistances: AME 0.06, ALE 0.09, PME 0.10, PLE 0.09; AME-AME 0.05, AME-ALE 0.01, PME-PME 0.01, PME-PLE 0.03, ALE-PLE 0.03; MOQ length 0.22, front width 0.17, back width 0.21. TA small, lobular, EP prolonged retrolaterad of EMB (Fig. 1); RTA bent at right angle above glabrous depression on retrolateral surface of tibia (Fig. 2). Leg spination typical for genus.

Female.—Total length 2.87. Carapace 1.37 long, 1.11 wide. Femur II 0.87 long. Eye sizes and interdistances: AME 0.05, ALE 0.07, PME 0.10, PLE 0.09; AME-AME 0.06, AME-ALE 0.01, PME-PME 0.01, PME-PLE 0.03, ALE-PLE 0.04; MOQ length 0.20, front width 0.16, back width 0.21. MP almost square (Fig. 3);



Figures 1-4.—*Drassyllus orlando*, new species: 1, palp, ventral view; 2, palp, retrolateral view; 3, epigynum, ventral view; 4, epigynum, dorsal view.

MED and AED widely separated (Fig. 4). Leg spination: femora: II p0-0-0; IV p0-0-0.

Other material examined.—Three males taken with the types (AMNH).

Distribution.—Known only from the type locality.

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SPERM DEPLETION IN THE ORB-WEAVING SPIDER *NEPHILA CLAVIPES* (ARANEAE, ARANEIDAE)

In the spider literature, it is generally assumed that individual males can and do inseminate more than one female. This would appear to be adaptive from the male point of view, particularly since spider males invest nothing in care of egg sac or young, and, in all three species examined so far, it seems that the first male to mate with a given female fertilizes most of her eggs (Austad 1984; Christenson and Cohn 1988). If a male defended a juvenile female for a period of time and then mated with her just after her final molt, he might well be expected to search for and mate with another female. However, the data showing that male spiders can inseminate that second female are sparse. Breene and Sweet (1985) have

demonstrated that male black widow spiders can inseminate at least three females. In this study, the limitation on insemination was determined by placing male *Nephila clavipes* (L.) with up to three sexually receptive virgin females and later examining both sexes for the presence of sperm. It would seem that any assessment of male tactics, in any species, would benefit from taking into account such information.

A number of ante-penultimate females (18-21 mm cephalothorax-abdomen length) and newly-molted adult males (7-9 mm cephalothorax-abdomen length) were gathered in July of 1986. To insure males were virgin, I gathered only those on orbs with sperm webs and with the newly-molted animal's coloration (see Myers and Christenson 1988). All subjects were housed in 123 x 62 x 62 cm boxes screened with Fiberglas®. These were situated in the hardwood forest at the F. Edward Hebert Center of Tulane University, located about 20 km outside of New Orleans, La. Females were fed two mealworm larvae per day.

Males were held in the field boxes, in male groups, for a few days to a week prior to presentation to a female. About two days before the female's molt, determined by pattern of web deterioration, each virgin male ($n = 11$) was placed in the upper barrier strands of a female's orb. After the female's molt, mating behavior was time sampled at about ten-minute intervals for two hours. This is sufficient observation to determine the nature of mating as copulations are frequent after the female's final molt, occurring an average of 28 minutes out of the hour for more than a day (Christenson et al. 1985). Males were removed from the first female's web at different times, ranging from 5 to 35 days after the female's molt. Time of removal varied in order to increase the longevity of some males, and to allow some males ($n = 3$) to mate with three females, and as a consequence of availability of females who were ready to molt. After male removal, first females ($n = 11$) were sacrificed, and the spermathecae removed, squashed, and examined with a phase contrast microscope for sperm. Female maturity was verified for each female by the sclerotized condition of the spermathecae.

Immediately after removal from the first female's cage, each male ($n = 11$) was placed with a second female in the manner already described. Second females molted anywhere from 10 to 34 days after the first female. On the day of second female molt, mating behavior was observed during a one-hour serial record, to give a more accurate account of mating frequency and time. Eight males were removed and the palps checked for sperm. Second females ($n = 11$) were removed and spermathecae checked in the manner already described.

The remaining three males were placed with a third female; those females molted 47, 51, and 53 days after the first females. Mating was observed for one hour after the female's molt. The three males and females were removed a few days after her molt and were checked for sperm. So, the eleven males had been sacrificed and checked for sperm between 2 and 9 weeks after molting to adulthood. This is about as long as adult male *N. clavipes* live under these captive conditions (Cohn and Christenson 1987) and probably much longer than they live under unrestrained conditions. To be included in the following analysis, the male and all females he mated with had to have been examined for sperm. Due to deaths and a few possible male escapes, data for an additional 8 males and 15 females were excluded.

Nine of the eleven males were observed to mate with the first female. Mating was of the usual vigor noted in *N. clavipes* just after the female's final molt (Christenson et al. 1985); mating was noted in 60% of the time samples and bulb contraction frequencies averaged 41 per min. Insertions of the conductor were numerous, and prolonged hematodochal bulb contractions were evident. All of the eleven first females' spermathecae contained many sperm.

Seven of the eleven males demonstrated some level of sexual behavior with the second female. However, the vigor of mating was relatively low. Prolonged conductor insertion with rhythmic and countable hematodochal bulb contractions occurred in only two cases. In the first, the male mated eight times for a total of 16 minutes; the bulb contraction rate was 30 per min. In the second, the male mated three times for almost 20 minutes; bulb contraction rate was 8 per min. The matings of five males included an average of seven brief conductor insertions with intermittent bulb contractions, the frequency of which were impossible to count. None of the 11 second females' spermathecae contained sperm.

None of the males with a third female showed any mating behavior. Third females contained no sperm. Eventually, all 11 males tested were sacrificed; none of their palps contained sperm. No sperm webs were noted in any female orb.

One can not take for granted that an active male spider can inseminate more than one female. Robinson and Robinson (1980) noted that eunuchs, males with terminal portions of the palps broken off, still actively fight with one another while on a female's orb. Although embolus damage is commonly thought to reduce or eliminate the ability to transfer sperm (Foelix 1982), it should be pointed out that Breene and Sweet (1985) found that even with damage to the tip of the embolus, male black widows were capable of inseminating the female. When a male *N. clavipes* mates, that does not necessarily mean that the male has sperm available to the female. Two males in this study demonstrated mating with a second female that could easily have been confused with mating typical of the day after the female's final molt (Christenson et al. 1985). The intermittent insertions and bulb contractions noted in five other males could have been confused with mating typically noted with older adult females (ibid.).

No sperm were found in the palps of any of the 11 males. This was somewhat surprising; we had suggested at one time that because males near the hub (and thus the female) had a feeding advantage over males remaining on the web periphery, the hub male would have a relatively greater chance of moving to and then mating with a second female (Christenson and Goist 1979). Anyway, it is unclear why no sperm were available. Perhaps spermatogenesis is terminated at the final molt, or there is some constraint on sperm transfer via sperm web construction or via prolonged copulations (up to 48 hours; Christenson et al. 1985) leading to embolus damage which in this species might inhibit sperm transfer. These possibilities are being examined histologically.

One might expect males of *N. clavipes* to be somewhat choosy concerning females that could be assessed at the time of their final molt. I do not think that males have an ample opportunity to do so. First, our boxed females do not attract males, indicating that molting females do not appear to produce a distance-acting pheromone, as can happen in other species (Olive 1982). Second, males have a limited opportunity to visit adult females inhabiting aggregated webs. Female *N. clavipes* aggregate later in the season, after having matured and

mated for the first time (Brown et al. 1985). Further study of male choice is, however, warranted.

The discussion of alternative mating tactics in spiders must include limitations on insemination. Consider what is perhaps the most fundamental decision a male orb-weaving spider has to make, to remain on a female web or to search for another female. Austad (1984) has argued that phyletic constraints, such as the structure of the female sperm uptake and storage anatomy, may be closely related to whether the male should guard the female. Results of the present study indicate that constraints relating to insemination limits should also be considered. Male *N. clavipes* deplete sperm after mating with a newly-molted female but do not leave to search. Most remain with the female after mating (Cohn et al. 1988). There is no compelling reason for males to leave their mate and search for another because they could not father additional offspring by doing so. The comparative study of spider species whose males routinely show limited guarding and frequent movement between females would clarify the importance of insemination limitation in the prediction of male behavioral tactics.

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FIELD OBSERVATIONS OF *GASTERACANTHA CANCRIFORMIS* (ARANEAE, ARANEIDAE) IN A FLORIDA MANGROVE STAND

Gasteracantha cancriformis (L.), sometimes known as the spiny-bellied orbweaver, is a tropical-subtropical spider in the Americas (Levi and Levi 1968). The biology of this spider is discussed in limited detail by Comstock (1940), Gertsch (1979), and Kaston (1978). Muma (1971) presents detailed observations on the seasonal history, web construction, mating, egg case construction, and spiderling activity. However, most of Muma's (1971) behavioral observations were made in the laboratory, and he does not quantify web components. This note quantifies the spider's web components and describes some of its field behavior and ecology.

Observations were conducted in 1975 from June to Sept. at the west end of the Howard Franklin Bridge and Fla. Hwy 688, Pinellas Co., Florida, in a stand of mixed mangroves, *Avicennia germinans* (L.) L., and *Rhizophora mangle* L. Approximately 58 h were spent in observing 41 subadults and adult females. Web component nomenclature is based on Savory (1977).

The $\bar{x} \pm \text{SD}$ (n) of various web characteristics were as follows: web diameter, $29 \text{ cm} \pm 6 \text{ cm}$ (19); web angle, $71.3^\circ \pm 11.5^\circ$ (20); spirals, 37.4 ± 7.5 (18); radii, 27.4 ± 6.5 (20); frame threads, 2.8 ± 0.9 (13); mooring threads, 3.8 ± 1.0 (19); bridge length, $1.1 \text{ m} \pm 0.5 \text{ m}$ (23); radii with flocculent silk tufts, 2.9 ± 1.8 (26); split radii with flocculent silk tufts, 1.0 ± 0.0 (3); frame thread with reinforced silk layers, 2.2 ± 0.6 (11); and mooring thread with reinforced silk layers, 2.0 ± 0.0 (2). Muma (1971) reported 20 to 30 radii which agrees with my findings. He reported also 10 to 30 spirals which is slightly less than what I observed. Levi and Levi (1968) showed flocculent silk tufts on the spiral and radii. Neither Comstock (1940), Muma (1971), nor I found these tufts on spirals. These tufts, or silken adornments, are probably protective devices that warn birds or large insects of a web's presence (Ewer 1972; Eisner and Nowicki 1983).

Muma (1971) reported that webs are constructed at an angle perpendicular to the ground, which I noted also. Females occupied the acute side of the incline and were positioned at the hub so that their black ventral surface faced up and their colored dorsal surface faced down. This may have been a counter-shading device or a thermoregulatory response.

On three separate occasions all spiders dismantled their webs just before or during rain, usually leaving from half of the web to only the bridge. This response to rain is similar to that of *Nephila maculata* (Fab.) (Robinson and Robinson 1973). When dismantling the web, *C. cancriformis* collected the silk and pressed it to her mouth, where she rolled it into a lump. The silk color changed from white to brown. Afterwards, the brownish lump was placed onto a part of the old web, on vegetation, or dropped. This color change suggests that rather than simply removing moisture from the silk, the spider may have extracted nutrients before discarding the silk.

Prey items included three mosquitoes (Culicidae), a horsefly (Tabanidae), a moth (Lepidoptera), two love bugs (Bibionidae), a small unidentified spider, an antlion (Myrmeleontidae), three honey bees (Apidae), and a fly (Muscidae). One female was observed drinking water after a rain storm by stroking her ventral abdomen with her left fourth leg and pressing the leg to her mouth; she did this

twice. One spider ate the pollen from the corbicula of a bee's leg. Juvenile orb-weaving spiders eat pollen (Smith and Mommsen 1984), but this is the first account of an adult spider eating pollen.

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SPIDER PREDATION ON VELVETBEAN CATEPILLAR MOTHS (LEPIDOPTERA, NOCTUIDAE) IN A SOYBEAN FIELD

The velvetbean caterpillar (VBC), *Anticarsia gemmatilis* Hübner, is a major pest of soybean (*Glycine max* [L.] Merrill) in the Gulf Coast area of the United States (Herzog and Todd 1980). Little is known about predators of VBC adults: Watson (1915, 1916) reported dragonflies in Florida but gave no names; Neal (1974) listed the green jacket dragonfly, *Erythemis simplicicollis* (Say), and the striped earwig, *Labidura riparia* (Pallas), in Florida; and Gregory (1987) reported the spider *Eriophora edax* (Blackwall) in Honduras. This note provides further documentation of VBC adult predation by spiders.

Observations were conducted by the senior author from 1981-1983 at the University of Florida's Green Acres Research Farm, Alachua County, FL. The study site was an approximately 1 ha soybean field (variety Bragg). Most observations were recorded to the nearest minute. Approximately 354 h were

Table 1.—Records of spider predation on adult velvetbean caterpillar (VBC) at the Green Acres Research Farm, Alachua County, FL (1981-1983). If exact time not given, then predation record occurred during hyphenated times. E = field edge (± 1 m), I = in field. Grass = unidentified grass, bahiagrass = *Paspalum notatum* Flugge, hairy indigo = *Indigofera hirsuta* L., soybean = *Glycine max* (L.) Merr., beggarweed = *Desmodium tortuosum* (Sw.) DC., sicklepod = *Cassia obtusifolia* L., Florida pusley = *Richardia scabra* L., sandbur = *Cenchrus* sp. With regard to VBC sex, A = undetermined, M = male, and F = female.

Species	Date	Time	Location	Substrate	VBC sex
<i>Peucetia viridans</i> (Hentz)	19 Sep. 81	2047	E	Bahiagrass	M
	19 Sep. 81	2058	I	Soybean	M
	24 Sep. 82	2112	I	Florida pusley	M
	17 Sep. 81	2115	E	Bahiagrass	F
	19 Sep. 83	2130	E	Sandbur	M
	24 Sep. 82	2147	I	Soybean	F
	24 Sep. 82	2223	I	Soybean	F
	09 Sep. 81	2303	I	Soybean	M
	03 Sep. 82	2323	E	Beggarweed	M
	03 Sep. 82	2340	I	Sicklepod	M
	25 Sep. 82	0023	I	Hairy indigo	M
	04 Sep. 82	0052	I	Soybean	M
	04 Sep. 82	0111	I	Sicklepod	M
	04 Sep. 82	0136	I	Soybean	M
	21 Aug. 81	0545-0701	I	Soybean	A
	25 Aug. 81	0545-0703	E	Grass	M
	15 Sep. 81	0545-0714	I	Soybean	M
<i>Misumenops celer</i> (Hentz)	03 Sep. 81	2230	E	Bahiagrass	M
	16 Aug. 81	0000-0700	E	Grass	M
	09 Oct. 82	0530	E	Hairy indigo	M
	01 Sep. 81	0545-0607	E	Grass	F
<i>Misumenoides formocipes</i> (Walck.)	15 Sep. 81	0545-0714	E	Bahiagrass	M
<i>Eriophora ravilla</i> (C. L. Koch)	17 Sep. 81	2100	I	Soybean	M
<i>Neoscona arabesca</i> (Walck.)	24 Sep. 82	2332	E	Soybean	M
	05 Oct. 82	0550	E	Soybean	F
<i>Acanthepeira</i> sp.	15 Sep. 83	0200	E	Bahiagrass	F

spent in the field during July through October, with 201 h during the day and 153 h during the night. Data were gathered by walking through the study site in a systematic fashion. Small sections of the field, and the associated arthropods, were disturbed during the day in the completion of other experiments; this may have reduced the number of observed kills. A six-volt Everready® Freedom Light™ was used for nocturnal observations; the lighting fixture was covered with a section of Zip-a-Tone color sheet, Vermillion Hue #2545.

Six species of spiders are documented for the first time as predators of VBC adults (Table 1). All 26 instances of predation were observed at night. The green lynx spider, *Peucetia viridans* (Hentz), accounted for 65% of the records; crab spiders (*Misumenops*, *Misumenoides*) for 19%; and orbweavers (*Acanthepeira*, *Eriophora*, *Neoscona*) for 15%. Eighty-two percent of records for *P. viridans* occurred between 2047 and 0136 hours, the time when VBC adults are most active (Gregory 1986). *Peucetia viridans* was found throughout the field, usually on dicotyledons and high above the ground (ca 1 m or higher). Crab spiders were found only at the field edge, usually on monocotyledons and close to the ground (ca 0.5 m or less). Most orbweavers were found at the field edge.

Twenty of the 26 captured moths were VBC males, a significant prey bias ($\chi^2=7.84$, $df=1$, $P<0.01$). Velvetbean caterpillar adult sex-ratio was ca 1:1 at the study site (Gregory 1986). The nature of the prey bias may be due to aggressive chemical mimicry of VBC mating pheromone by some of these spiders (see Foelix 1982). Based on the predation records, spiders were the principal mortality agents of VBC adults; no other predators were observed at the study site.

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WATER-RESISTANT SEX PHEROMONES IN LYCOSID SPIDERS FROM A TROPICAL WET FOREST

The role of female sex pheromones for pre-copulatory communication in lycosid spiders has been studied in Nearctic and Palearctic species that inhabit deciduous forest and grassland biomes (review in Tietjen and Rovner 1982). Substances involved are often bound to the silk dragline secreted by the female as

she wanders (Engelhardt 1964; Tietjen 1977; Tietjen and Rovner 1980), deposited on the substratum (Bristowe and Locket 1926; Richter et al. 1971), or released into the air (Tietjen 1979). The findings on another family of wandering spiders, the Salticidae, recently have been reviewed (Pollard et al. 1987).

In the lycosids studied so far, the substances serving as contact sex pheromones are inactivated (i.e., become ineffective for stimulating males) by water (Dondale and Hegdekar 1973; Tietjen 1977). Consequently, rain or dew can limit the use of such chemical signals in these spiders. On the other hand, *Dolomedes triton* (Walckenaer), a member of the closely related family Pisauridae, produces a sex pheromone that is effective on water, reflecting the special needs of this semi-aquatic spider (Roland and Rovner 1983).

In lycosids that inhabit a tropical wet forest life zone, where there is nightly dew and frequent rainfall, any substrate-deposited or silk-bound pheromone that could be effective for some hours would be expected to resist inactivation by water. We tested this hypothesis in two species of lycosids, *Lycosa tristani* Banks (at one time placed in the genus *Schizocosa*) and *Lycosa longitarsis* F. Pickard-Cambridge (a member of the *Lycosa helluo* species group). (Voucher specimens of both species are deposited at the Biosystematics Research Centre in Ottawa). Both lycosids were abundant when collected at night as they rested waiting for prey in a mown clearing at the Organization for Tropical Studies' La Selva research station near Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica. Research was conducted from mid-November through late December, 1987.

While male spiders placed in vacated female cages usually showed courtship display, those placed in the vacated cages of females which had their spinnerets sealed with paraffin rarely did so (Table 1). Presumably, the female pheromone was bound to the silk, not deposited directly on the substrate by tarsal or body contact. There was little or no courtship response by males to the vacated cages of other males (*L. tristani*, 1/10; *L. longitarsis*, 0/10).

Next, males were tested with female draglines subjected to various treatments. Tethered females were led along a cardboard track, traversing three glass rods (5 mm diameter) placed 7 cm apart and perpendicular to the path of the spider. The dragline began at an attachment disk and was fastened at the other end with adhesive tape. The taut and slightly elevated dragline was then either untreated, allowed to age for 1 day, misted with water and allowed to dry, submerged in water and allowed to dry after removal of the water from the tray, misted with ethanol and allowed to dry, or misted with hexane and allowed to dry. (Drying time was at least 0.5 h in all cases.) Male *L. longitarsis* also were tested with untreated male draglines obtained in a similar manner to those of females. (Male draglines of *L. tristani*, a much smaller lycosid, were not tested because the males did not leave a sufficiently thick dragline as they were led along the track. Female

Table 1.—Occurrences of male courtship behavior in vacated cages of female conspecific lycosid spiders with or without sealed spinnerets. Significance of differences: *G*-test with Yates' correction. **P* < 0.05; ****P* < 0.001.

Spinnerets	<i>Lycosa longitarsis</i>	<i>Lycosa tristani</i>
Sealed	2/20 <i>G</i> = 5.820*	0/10 <i>G</i> = 19.782***
Not sealed	6/10	10/10

Table 2.—Number of males showing courtship display and dragline-following in response to untreated or treated conspecific lycosid draglines. Values having asterisks are significantly different at the 0.05 (*), 0.01 (**), or 0.001 (***) levels from the within-column value for untreated female draglines (*G*-test with Yates' correction). *N* = 10 males of each species/test.

Dragline	Treatment	<i>Lycosa longitarsis</i>		<i>Lycosa tristani</i>	
		Court	Follow	Court	Follow
Female	Untreated	7	7	9	10
Female	1-day old	2	3	4	5*
Female	Water spray	5	8	10	7
Female	Underwater	6	8	—	—
Female	Ethanol spray	2	3	7	8
Female	Hexane spray	1*	1*	1**	1***
Male	Untreated	0**	0**	—	—

draglines of *L. tristani* were not tested after being submerged, since they broke too easily when the water was removed from the tray.)

The results of the above-listed tests are given in Table 2. The two lycosids not only responded to the female pheromone by courting, but also showed dragline-following, as in previously studied lycosids. (Neither response occurred when draglines of male *L. longitarsis* were tested.) Loss of stimulatory efficacy with time, perhaps due to volatility of the pheromone, was suggested by lower male responsiveness toward 1-day-old lines, significant in one category. Subjecting the female draglines to water—even submergence—did not reduce the response levels of the males significantly, nor did spraying the lines with ethanol. Male responsiveness in both species was reduced significantly after the lines were sprayed with hexane, which, unlike water or ethanol, adhered to the silk. Apparently, the dragline-bound pheromones of these lycosids are non-polar compounds (being inactivated by hexane) and probably are not washed off or inactivated by the nightly dew and frequent rain that typifies the tropical wet forest life zone.

Our observations that penultimate male and female *L. longitarsis* constructed dome-shaped nests in their cages before molting led to additional study of this species. (Nest construction also was observed in some adult females with, as well as without, egg sacs, although these nests appeared less dense than those used by penultimate instars for molting.) We tested the nests of penultimate females for possible stimulatory value by placing adult males in the vacated cages of such females. Seven of 20 males tested showed courtship after contacting the nest. This was not significantly different from the response level (6/10) shown by these males to the vacated cages of adult females (*G* = 0.688). The construction of nests with a sex pheromone bound to the silk is a behavior not reported before in subadult lycosids, although it is well known in other families of wandering spiders (Tietjen and Rovner 1982; Pollard et al. 1987). The presence of female sex pheromone in penultimate female *L. longitarsis* also was suggested by the attempts of four out of ten adult males to copulate with freshly killed penultimate females.

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DESCRIPTION OF THE MALE OF *ARANEUS COCHISE* (ARANEAE, ARANEIDAE)

Levi (1973) described *Araneus cochise* from a single female collected at the Southwestern Research Station in the Chiricahua Mountains of Arizona. The species was placed in the *Araneus sturmi* group. The *A. pegnia* and *A. sturmi* groups include most of the small species of *Araneus*. Recently *A. cochise* was recorded from Texas (Agnew et al. 1985) based on some females swept from *Juniperus ashei* Buchholz near Stephenville in 1982. More extensive collecting the following spring yielded a larger series including males of *Araneus cochise* which are described here for the first time.

The collection area consists of *J. ashei* and other shrubs in a landscape of rocky hillsides. This habitat is located in the western section of the Cross Timbers region of Texas (elevation = 399 m). The region grades from open grass savannah



Figures 1, 2.—*Araneus cochise* left palp: 1, ventral view; 2, mesal view. Scale = 0.5 mm.

to dense brush of post oak (*Quercus stellata* Wangenheim) and blackjack oak (*Quercus marilandica* Muenchhausen).

Araneus cochise Levi

Figs. 1, 2

Araneus cochise Levi, 1973, p. 497, figs. 55-59, map 2 (female holotype from Cochise County, Arizona, in American Museum of Natural History).

Diagnosis.—The male of *A. cochise* keys to *A. mariposa* Levi because the conductor has a notch and tooth on the middle of the lateral side but differs from the latter in that the median apophysis is more curved (Figs. 1, 2). A black stripe extends from the middle anterior portion of the abdomen posteriorly to the humps and branches outward to the folium which is more distinct than in other *Araneus*. Markings in the female are similar to those of the male.

Description (Male).—The carapace and abdomen are similar to the female except that the black longitudinal stripe on the anterior part of the abdomen is more pronounced. Measurements of 15 specimens (mm): Total length (\bar{x} = 2.87, range = 2.5-3.3, SE = 0.05); carapace length (\bar{x} = 1.58, range = 1.5-1.7, SE = 0.01), width (\bar{x} = 1.41, range = 1.4-1.5, SE = 0.01); first femur (\bar{x} = 1.74, range = 1.6-2.1, SE = 0.03); patella and tibia (\bar{x} = 1.97, range = 1.9-2.1, SE = 0.02); metatarsus (\bar{x} = 1.33, range = 1.2-1.6, SE = 0.03); tarsus (\bar{x} = 0.61, range = 0.6-0.7, SE = 0.01). Second patella and tibia (\bar{x} = 1.76, range = 1.6-1.9, SE = 0.02); third (\bar{x} = 0.97, range = 0.9-1.0, SE = 0.01); fourth (\bar{x} = 1.31, range = 1.2-1.4, SE = 0.02).

Description (Female).—Measurements of 33 specimens (mm): Total length (\bar{x} = 3.59, range = 2.8-4.3, SE = 0.06); carapace length (\bar{x} = 1.56, range = 1.4-1.7, SE = 0.01), width (\bar{x} = 1.36, range = 1.3-1.5, SE = 0.01); first femur (\bar{x} = 1.54, range = 1.4-1.7, SE = 0.01); patella and tibia (\bar{x} = 1.75, range = 1.6-2.0, SE = 0.02); metatarsus (\bar{x} = 1.02, range = 1.0-1.1, SE = 0.01); tarsus (\bar{x} = 0.52, range = 0.5-0.6, SE = 0.01). Second patella and tibia (\bar{x} = 1.51, range = 1.4-1.7, SE = 0.01); third

(\bar{x} = 0.92, range = 0.9-1.0, SE = 0.01); fourth (\bar{x} = 1.29, range = 1.2-1.4, SE = 0.01).

Record.—TEXAS; *Erath Co.*, 11 km NE of Stephenville (C. W. Agnew, American Museum of Natural History, Museum of Comparative Zoology, Texas A&M University).

Note.—Males and females were first collected on 11 April. Males were last collected on 16 May and females occurred until 10 June. One egg sac was found and 7 spiderlings emerged.

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Research Notes

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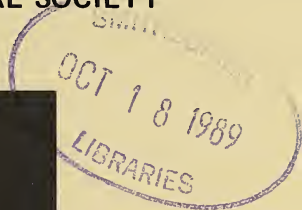
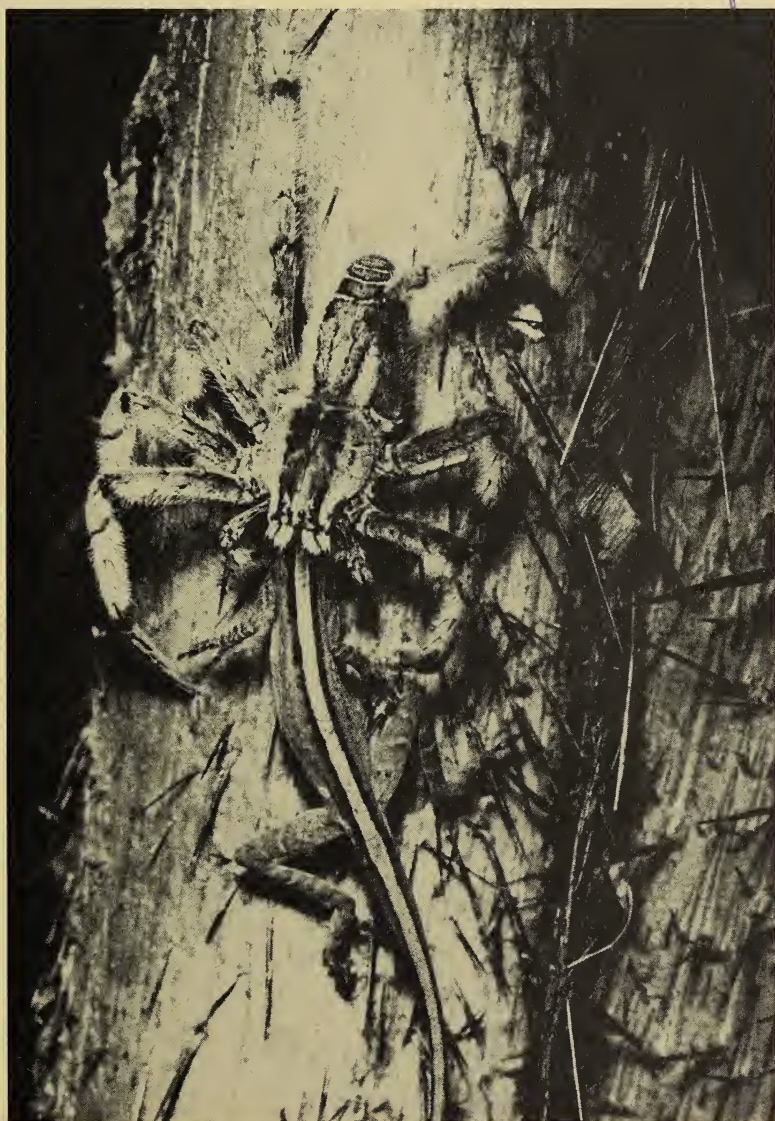
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La Selva Biological Station of OTS, Costa Rica, by J. S. Rovner
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ANALISIS DEL COMPORTAMIENTO SEXUAL Y PRODUCCION DE OOTECAS DE *THERIDION RUFIPES* (ARANEAE, THERIDIIDAE)¹

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ABSTRACT

This paper deals with a laboratory study of the sexual behavior of *Theridion rufipes*. Thirty males and 30 females were reared individually from the egg stage. Precopulatory, copulatory and postcopulatory behaviors were described. Behavior patterns of the male were examined, describing in detail the 16 observed units. Females adopted a passive attitude during copulation. The positions adopted by the male and female were drawn during the process. Thirty couples were observed; in 27, copulation took place. The number of egg depositions by each fertilized female is given, as well as the percentage of fertility and fecundity, the higher percentage occurring in the first egg sacs constructed.

EXTRACTO

En el presente trabajo se realizó el estudio del comportamiento sexual en el laboratorio de *Theridion rufipes*. Se utilizaron 30 machos y 30 hembras criadas en el laboratorio individualmente desde el estado de huevo. Se describieron las unidades de comportamiento precopulatorio, copulatorio y postcopulatorio. Se confeccionó el patrón de comportamiento de macho, describiéndose en detalle las 16 unidades observadas. No se confeccionó el patrón correspondiente al comportamiento de la hembra porque ésta asumió una actitud pasiva durante toda la experiencia. Se graficaron las cuatro posiciones adoptadas por el macho y la hembra durante el proceso. De los 30 casos observados, en 27 se produjo cópula. Se dio a conocer el número de desoves realizados por hembra fecundada, el que osciló entre 3 y 9 ($\bar{x} = 4$) y el porcentaje de fertilidad y fecundidad, correspondiéndole mayor porcentaje a las primeras ootecas construidas.

INTRODUCCION

En el presente trabajo se realiza el estudio del comportamiento sexual en el laboratorio de *Theridion rufipes* Lucas. Se describen las unidades de comportamiento observadas durante los períodos precopulatorio, copulatorio y postcopulatorio. Se da a conocer el número de desoves obtenido por hembra fecundada, el intervalo entre las puestas, la edad máxima de los ejemplares en su primer desove, la edad máxima en que puede desovar, la vida reproductiva y la vida fértil y los porcentajes de fecundidad y fertilidad.

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MATERIAL Y METODOS

Para realizar el estudio del comportamiento precopulatorio, copulatorio, postcopulatorio y desoves, se utilizaron 30 machos y 30 hembras criadas en el laboratorio individualmente desde el estado de huevo, según métodos explicados en una publicación anterior (González 1979).

Los ejemplares empleados en esta experiencia fueron seleccionados cinco días después de su muda de maduración. Cada hembra fue colocada en recipientes de vidrio de 25 x 15 x 15 cm tres días antes de la introducción del macho. Se impidió que los individuos se vieran entre sí.

Las observaciones se efectuaron bajo las siguientes condiciones de laboratorio: temperatura $23^{\circ}\text{C} \pm 3$, fotoperíodo de extensión normal entre 12 y 14 hs diarias de luz natural y humedad relativa del 60% al 70%.

Los machos elegidos al azar fueron introducidos cuidadosamente en los recipientes donde se hallaban las hembras y por un lugar opuesto al de ellas.

La denominación de las unidades y de las series de movimientos están en parte inspirados en Costa (1975, 1979).

RESULTADOS

Comportamiento precopulatorio.—Al introducir el macho en el recipiente de la hembra ambos permanecen inmóviles por el término de 2 a 5 minutos. Luego, el macho suspendido de la tela y sin desplazarse del lugar en que se encuentra, efectúa una serie de movimientos (abajo-arriba) con los extremos de los tarsos en forma alternada (derecho e izquierdo) y formando un ángulo mayor de 90° y menor de 120° con la articulación fémoro-patelar.

Conjuntamente con el movimiento de los palpos, el macho ejecuta movimientos lentos (sacudidas) arriba-abajo, adelante-atrás con el primer par de patas sin llegar a tocar la tela, formando un ángulo abierto (más de 100°) con la articulación fémoro-patelar en el movimiento arriba-abajo y un ángulo agudo (menos de 90°) en el movimiento adelante-atrás.

El tiempo empleado en ejecutar estos dos movimientos es breve, aproximadamente de 60 a 70 segundos, durante los cuales no se observó ningún movimiento abdominal.

Seguidamente, el macho detecta la presencia de la hembra y comienza un lento desplazamiento hacia ella, que se mantiene suspendida de la tela con el dorso hacia abajo. El macho avanza siguiendo una misma dirección en forma cautelosa. Robinson (1982) explica esto mediante la presencia de feromonas aéreas y de líneas de arrastre dejadas por la hembra y seguidas mecánicamente por el macho.

El macho se acerca hasta 1 cm de distancia de la hembra y se detiene (quietud) suspendido de la tela con el dorso hacia arriba y ejecuta movimientos con los palpos a modo de pedaleo (pedaleo palpar). Se alternan 50 a 60 segundos de pedaleo palpar con 30 a 40 segundos de quietud, observándose este proceso entre 9 y 15 veces.

La hembra hasta este momento ha permanecido inmóvil.—Finalizado el pedaleo palpar y al establecerse el contacto con el macho, la hembra, bruscamente, cambia de postura y se coloca suspendida de la tela verticalmente con el cefalotórax hacia abajo y la zona ventral hacia el macho. El macho

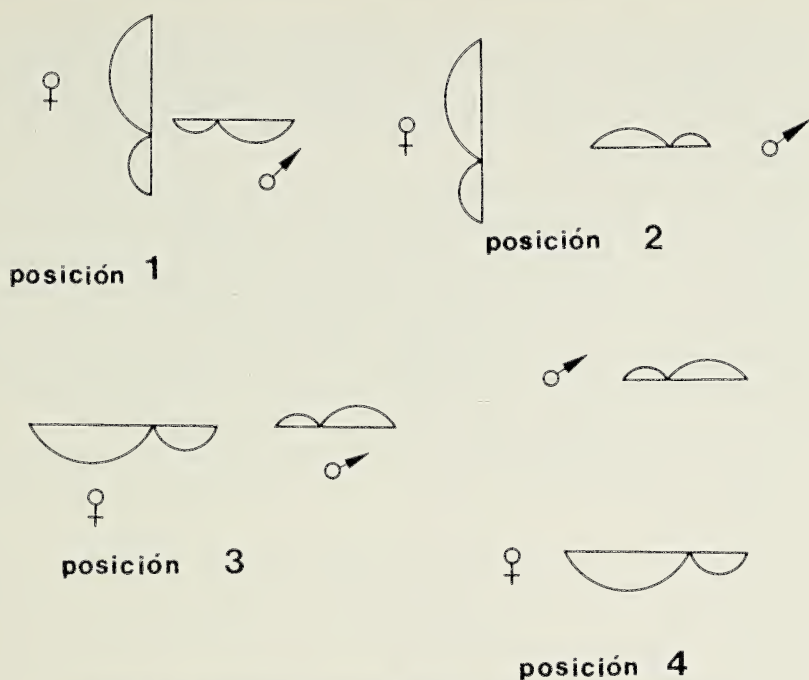


Figura 1.—Distintas posiciones adoptadas durante el apareamiento.

invierte su posición y se mantiene suspendido de la tela horizontalmente con la zona dorsal hacia abajo y el cefalotórax hacia la hembra (Fig. 1 - posición 1), quedando perpendicularmente uno con respecto al otro, de tal modo que los palpos del macho se hallan enfrentados a la zona epiginal de la hembra, es decir que adoptan la posición de cópula (toma de posición).

Lo descrito hasta aquí ha sido observado en 27 de los 30 casos estudiados; en los tres restantes, al realizarse el acercamiento del macho, las hembras se desplazaron rápidamente hacia el extremo opuesto del recipiente, no mostrándose receptivas a la cópula.

Comportamiento copulatorio.—En la posición 1, el macho extiende hacia adelante las patas 1 y 2 (derecha e izquierda) por debajo de la zona ocular de la hembra como abrazándola (abrazo) formando un ángulo de $100^\circ \pm$ con la articulación fémoro-patellar. Las patas 4 las mantiene extendidas hacia atrás en línea recta. Los palpos se hallan extendidos sin efectuar ningún movimiento. Acompaña al abrazo un movimiento rítmico de corto recorrido (arriba-abajo, adelante-atrás) del abdomen. Emplea entre 3 y 4 minutos para llevarlos a cabo con intervalos de quietud de 30 a 40 segundos.

Luego el macho frota sus palpos (frotamiento palpar) en forma alternada (derecho e izquierdo, indistintamente) sobre la zona del epigino de la hembra, sin desplazarse, por espacio de 1 a 3 minutos. Kaston (1970) para especies del género *Latrodectus* y González (1986) para *Steatoda retorta* describen un frotamiento similar. La hembra continúa inmóvil durante todo este tiempo.

Finalizado el frotamiento palpar se produce la cópula (inserción palpar). La inserción es alternada. Cuando un palpo es introducido en el orificio genital femenino, el opuesto se halla extendido en línea recta hacia arriba. Acompaña a la inserción un movimiento del abdomen. Al retirarse el palpo del epigino, el

macho manifiesta suaves movimientos abdominales de adelante-atrás y arriba-abajo (2 ó 3 segundos). La introducción es rítmica y dura de 2 a 4 minutos. Las primeras inserciones son más cortas que las últimas. El número de inserciones por cópula varía entre 4 y 12, son más numerosas en las primeras y van disminuyendo en las últimas.

Concluída una cópula los individuos de la pareja cambian de posición. El macho invierte la suya en un movimiento rápido, quedando con la zona dorsal hacia arriba, gira 180° se aleja 2 ó 3 cm (Fig. 1 - posición 2), gira nuevamente 180° y queda con el cefalotórax hacia la hembra nuevamente. La hembra se coloca horizontalmente con la zona dorsal hacia abajo y el cefalotórax dirigido hacia el macho (Fig. 1 - posición 3). Ambos ejemplares permanecen en posición 3 (enfrentados pero invertidos) sin manifestar movimientos (descanso) durante 2 ó 3 minutos, tras los cuales adoptan la posición 1 y se reinicia lo descripto.

Este proceso que comprende desde la toma de la posición 1 a la posición 3 con cópula incluída, se repite de 4 a 8 veces ($\bar{x} = 6$), empleando para ello desde 38 a 49 minutos ($\bar{x} = 41$).

Concluída la última cópula, el macho que estaba en posición 1 se desliza rápidamente hacia la zona superior del recipiente (retirada del macho) alejándose de la hembra y ubicándose por encima de ella, a más de 10 cm de distancia; inmediatamente invierte su posición quedando suspendido de la tela horizontalmente, con el dorso hacia arriba. La hembra adopta su posición habitual (horizontalmente con el dorso hacia abajo) (Fig. 1 - posición 4).

Comportamiento postcopulatorio.—El macho, luego de la retirada, se detiene (posición 4) y efectúa la limpieza de los palpos frotando uno contra otro (limpieza palpar), empleando en ello de 5 a 7 minutos; conjuntamente realiza movimientos bruscos con las patas 1 y 2 a modo de bicicleteo (bicicleteo pedial) y movimientos con el abdomen (movimientos abdominales) de arriba-abajo de corto recorrido,

En la Fig. 2 se halla representado el modelo total del comportamiento sexual tipo del macho de *Theridion rufipes*.

En el 78% de las parejas que copularon no se observaron nuevos acercamientos. En el 32% restante, entre los 33 y 39 minutos posteriores a la limpieza palpar, el macho se desplazó nuevamente hacia la hembra y se repitieron las etapas de quietud, pedaleo palpar y toma de posición del comportamiento precopulatorio y las etapas de abrazo, movimientos abdominales y frotamiento palpar del comportamiento copulatorio. Este último frotamiento palpar es más prolongado (2 a 5 minutos) y con un ritmo más acelerado que el de los primeros acercamientos. En ningún caso se produjo cópula, ya que finalizado el frotamiento palpar, la hembra que parecía receptiva, comienza a efectuar movimientos bruscos a modo de pedaleo con sus patas 1 y 2. Esto provoca el alejamiento inmediato del macho, cambiando ambos ejemplares de posición 1 a posición 4. Umaña (1987) también observa para la misma especie la existencia de una sola cópula al inicio de la vida adulta.

A partir de aquí, y a pesar de haber dejado conviviendo por más de quince días a las parejas en el mismo recipiente, no se registraron nuevos acercamientos ni actitudes de ataque.

Desoves, fecundidad y fertilidad.—Las hembras fecundadas en el laboratorio desovaron entre los 11 y 172 días ($\bar{x} = 72$ días) después del apareamiento. El total de ootecas construídas por las 27 hembras fecundadas fue de 132, y la

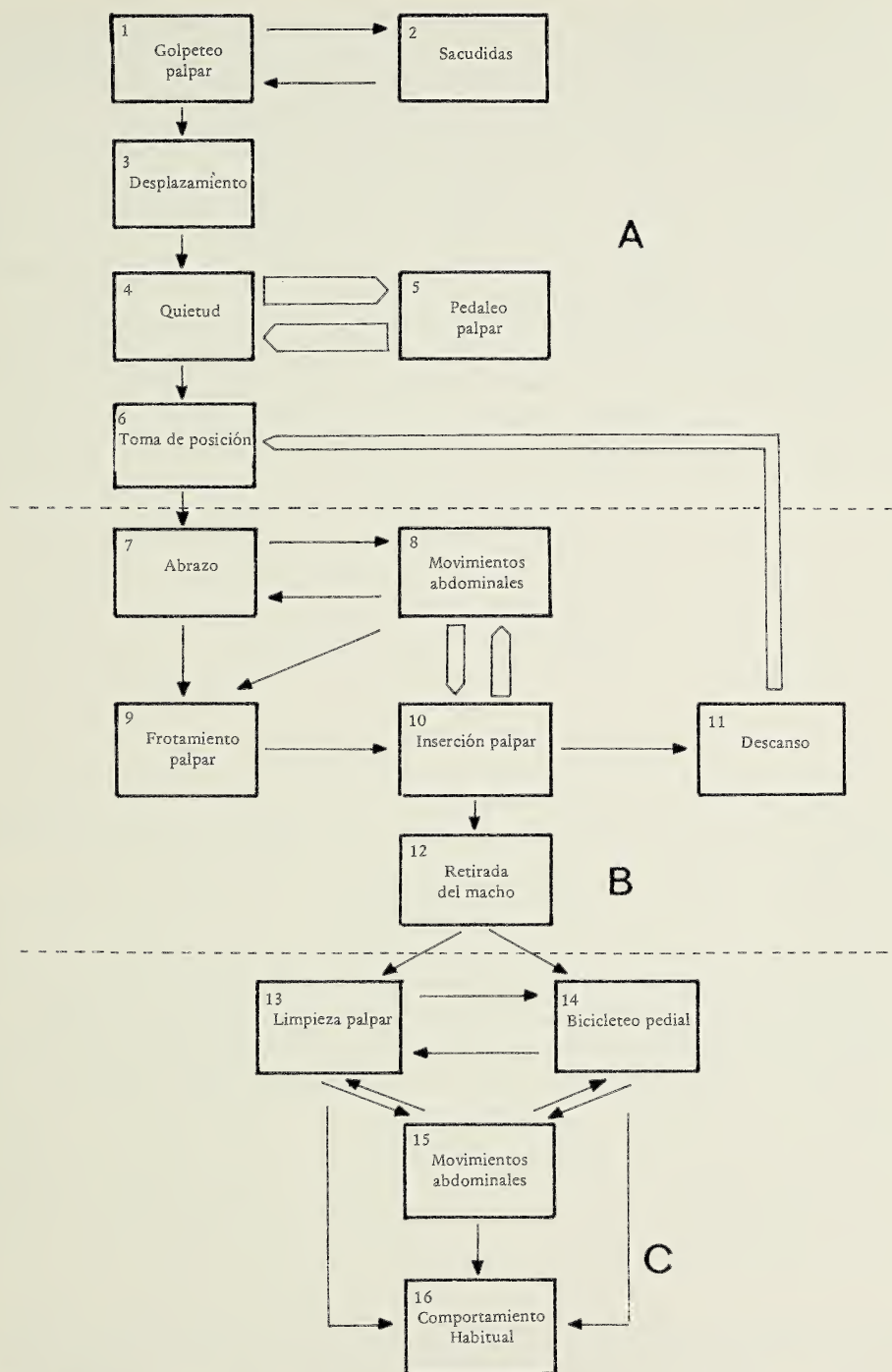


Figura 2.—Modelo tipo del comportamiento sexual del macho. Espesor de las flechas: 5 mm = 10 sucesiones. A = Comportamiento precopulatorio, B = Comportamiento copulatorio, C = Comportamiento postcopulatorio.



Figura 3.—Número de desoves por hembra.

cantidad de desoves por hembra fue variable, desde 3 a 9 ($\bar{x} = 4$) (Fig. 3). Según Umaña (1987) el número de ootecas construidas por hembra es de 1 a 10.

Teniendo en cuenta las hembras fecundadas y los desoves efectuados, se consideraron los siguientes períodos: a) eclosión y primer desove (edad del ejemplar en su primer desove), b) eclosión y último desove (edad máxima en que puede desovar), c) última muda y último desove (vida reproductiva), d) primera fecundación y último desove (vida fértil), e) último desove y muerte (Tabla 1).

Umaña (1987) proporciona datos sobre número de mudas, duración de estadíos y crecimiento. Debe tenerse en cuenta que esta autora llama "primera muda verdadera" que da origen a un segundo estadio a la muda que en el presente estudio, así como en otros anteriores (González 1979, 1981, 1982, 1984, 1986) se ha considerado como la tercer muda, que da lugar al cuarto estado (contando como primera muda el desprendimiento de la cutícula embrional que arrastra consigo al diente de eclosión).

Tabla 1.—Intervalos en días entre: a = eclosión y primer desove, b = eclosión y último desove, c = última muda y último desove, d = primera fecundación y último desove, e = último desove y muerte. N = número de individuos, \bar{x} = promedio, SD = desviación típica.

	a	b	c	d	e
N	27	27	27	27	27
A	228-305	322-500	130-276	83-254	186-265
\bar{x}	280.71	383.57	207.28	150.57	255.29
SD	32.50	55.87	45.41	56.54	26.07

Tabla 2.—Porcentaje de fecundidad (Fe) y de fertilidad (Fr). *N* = número de individuos, *A* = amplitud, \bar{x} = promedio, SD = desviación típica.

	Primeras ootecas		Últimas ootecas	
	Fe	Fr	Fe	Fr
<i>N</i>	10	10	10	10
<i>A</i>	107-71	107-70	73-78	70-32
SD	11.88	12.40	10.10	11.02
\bar{x}	93.5	89.7	56.9	52.5

El promedio de huevos por ooteca fue de 89, correspondiéndole a la primera el mayor número de huevos (107), el que fue descendiendo en las ootecas siguientes, siendo en la última de 38. Esto concuerda con lo citado por Umaña (1987).

Todos los huevos puestos no evolucionaron normalmente. En muy pocas ootecas el desarrollo de los huevos alcanzó el 100%, mientras que en la gran mayoría, el porcentaje de fecundidad (número de huevos puestos) es mayor que el porcentaje de fertilidad (número de huevos fértiles).

Kaston (1970) sostiene que para especies del género *Latrodectus* el porcentaje de fecundidad y de fertilidad no está en relación directa con el orden en que se producen los desoves, ya que ootecas construídas tempranamente pueden no mostrar desarrollo, mientras que otras construídas con posterioridad y por la misma madre, poseen gran número de huevos y alcanzan el mas alto porcentaje de fertilidad.

Esto no sucede con los desoves de *Theridion rufipes*. Los estudios efectuados demuestran que las primeras ootecas realizadas tienen mayor porcentaje de fertilidad que las realizadas mas tardiamente (Tabla 2), coincidiendo esto con los resultados de Umaña (1987).

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PACHYLOIDES HADES, NUEVA ESPECIE DE OPILIÓN DE LA ARGENTINA (OPILIONES, GONYLEPTIDAE, PACHYLINAE)

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ABSTRACT

Pachyloides hades, a new species of Gonyleptidae from the province of Tucumán, Argentina, is described and illustrated. It differs from its nearest relative, *Pachyloides tucumanus* Canals, mainly in the armature of the ocular tubercle and trochanter IV of the males. Differences from *Pachyloides thorellii* Holmberg and *Daguerreia maculata* Canals are also noted. *P. hades* was collected at two localities over 2,000 m above sea level.

RESUMEN

Se describe e ilustra *Pachyloides hades*, nueva especie de Gonyleptidae de la provincia de Tucumán, Argentina. Se comentan las diferencias con su especie más próxima, *Pachyloides tucumanus* Canals (principalmente referidas a la armadura del oculario y el trocánter IV del macho), así como con *Pachyloides thorellii* Holmberg y *Daguerreia maculata* Canals. *Pachyloides hades* fue colectada en dos localidades situadas por encima de 2,000 m s.n.m.

INTRODUCCIÓN

Revisando material de Gonyleptidae del noroeste argentino, perteneciente al Museo de La Plata, localicé dos machos, mal conservados, de una posible nueva especie, afín a *Pachyloides tucumanus* Canals. No obstante su parecido con ésta, los ejemplares mostraban algunas particularidades, pero en ese momento era difícil determinar si ellas obedecían a variaciones individuales. Esto me motivó a realizar un viaje a la localidad de tales especímenes (El Infiernillo, provincia de Tucumán), donde logré reunir un interesante lote. En proximidades de Tafí del Valle capturé otros ejemplares de la misma especie, en tanto obtuve lotes adicionales en las colecciones del Instituto Miguel Lillo de Tucumán. El estudio de este material me permitió confirmar la validez de la especie, que describo a continuación con el nombre de *Pachyloides hades*.

Con ésta suman seis las especies de *Pachyloides* Holmberg presentes en Argentina, totalizando unas 14 para el género, cuya área de distribución abarca también Uruguay, Paraguay y Brasil (Ringuelet 1959; Soares y Soares 1954). Algunas de estas especies necesitan una cuidadosa revisión de su status taxonómico, lo que será objeto de futuras contribuciones.

Pachyloides hades, nueva especie

Figs. 1-8

Daguerreia maculata: Meyer y Weyrauch, 1966:60 (Fig. 43), 61 (error de identificación).

Derivatio nominis.—El nombre específico *hades* (en aposición) refiere al dios de los infiernos en la mitología griega, en alusión a la localidad tipo.

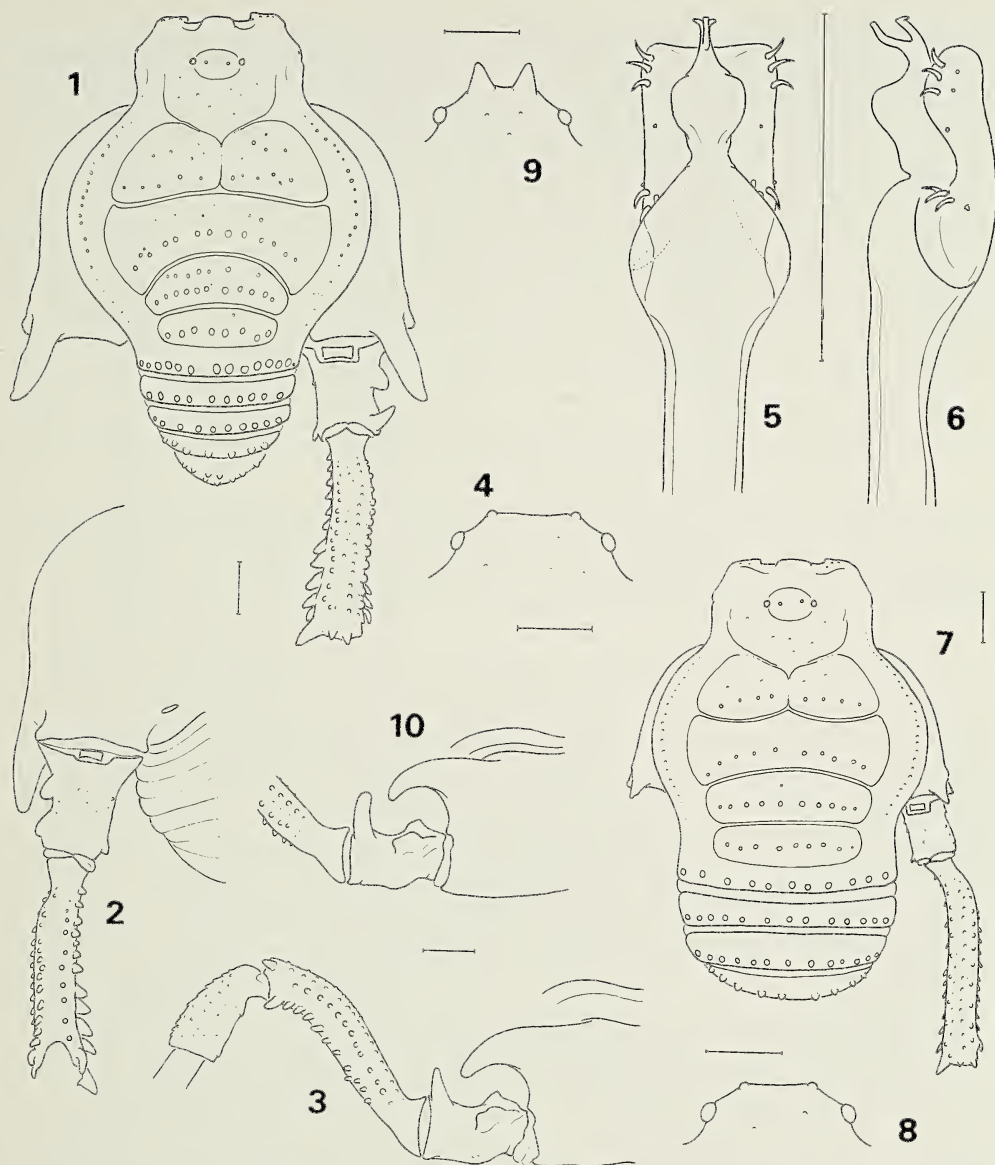
Material típico.—Holotipo macho (MACN 8620), El Infiernillo, Tucumán, 5 abril 1986 (L. Acosta); alotipo hembra, iguales datos, en el mismo tubo que el holotipo. Un macho y una hembra paratipos (CZI), igual localidad, fecha y colector; un macho y dos hembras paratipos (IML), igual localidad, 5 abril 1965 (W. Weyrauch); un macho y una hembra paratipos (MACN 8621), La Quebradita, Tafi del Valle, Tucumán, 4 abril 1986 (L. Acosta). El ejemplar macho de IML que aquí se designa como paratipo es presumiblemente el mismo individuo ilustrado en Meyer y Weyrauch (1966), con el nombre de *Daguerreia maculata* Canals.

Localidad tipo.—El Infiernillo (provincia de Tucumán, Argentina); 26°44'S/65°47'W.

Distribución geográfica.—Argentina, provincia de Tucumán. Hasta el momento, la especie ha sido colectada en dos localidades del sistema montañoso del Aconquija: El Infiernillo (3,042 m s.n.m.) y La Quebradita (2,100 m, próxima a Tafi del Valle). Desde el punto de vista biogeográfico ambas corresponden a la provincia altoandina (Cabrera y Willink 1973).

Habitat.—En sus dos localidades, *Pachyloides hades* fue hallada bajo piedras, en ambiente húmedo. El material de La Quebradita se colectó en las márgenes de un arroyo, bordeado por un bosquecillo de aliso (*Alnus jorullensis* H.B.K.); dicha localidad representa el límite superior para esta betulácea, que entre los 1,700 y 1,800 m forma un piso altitudinal, con bosques casi puros. El ambiente en El Infiernillo es, en cambio, un típico pastizal de altura, dominado por especies de *Festuca*. La precipitación pluvial es aquí inferior a los 400 mm anuales, pero son frecuentes las nieblas densas—especialmente al atardecer y la noche—, que al condensarse sobre la vegetación y las rocas, aseguran una importante cuota de humedad al sustrato (Meyer y Weyrauch 1966).

Descripción.—Coloración general pardo amarillento a castaño anaranjado, coxa y fémur IV más oscuros; pedipalpos, patas I a III y metatarso y tarso IV amarillo claro. Medidas de holotipo y alotipo en Tabla 1. Longitud del escudo dorsal: machos de 5.30 a 7.49 mm ($\bar{x} = 6.49$, $n = 14$), hembras de 6.06 a 6.98 mm ($\bar{x} = 6.45$, $n = 14$). Prosoma con escasos gránulos, dispersos y sobre el borde anterior; oculario bajo, con armadura representada por un par de gránulos o tubérculos muy pequeños. Escudo con surcos poco marcados, especialmente en el macho, el surco longitudinal en el área I puede faltar o estar apenas insinuado (en el holotipo este surco es muy tenue); en las hembras los surcos se destacan con franjas de pigmento levemente más oscuras. Pedipalpos: fémur con uno y trocánter con dos tubérculos setíferos ventrales, el primero con una espina subterminal mesial. Número de tarsitos: 6-8/9-7-7, con frecuencia el tarsito basal en pata I algo dilatado (holotipo con 6-8/9-7-7 tarsitos, alotipo con 6-8-7-7; variabilidad en Tabla 2). *Macho*: Granulación poco destacada en áreas I, II y laterales, más llamativa en las restantes áreas y los tergitos libres, con gránulos anchos y bajos. Área I con dos hileras irregulares de pocos gránulos; áreas II y



Figuras 1-8.—*Pachyloides hades*, nueva especie: 1-6, holotipo macho (MACN 8620); 1, escudo dorsal, tergitos libres, opérculo anal, coxas IV, trocánter y fémur derechos, vista dorsal; 2, coxa, trocánter y fémur IV derechos, vista ventral; 3, coxa, trocánter, fémur y patela IV derechos, vista lateral; 4, oculario, vista posterior; 5, pene, glándula en vista dorsal; 6, íd., vista lateral; 7-8, alotipo hembra (MACN 8620); 7, escudo dorsal, tergitos libres, coxas IV, trocánter y fémur derechos, vista dorsal; 8, oculario, vista posterior. Figuras 9-10.—*Pachyloides tucumanus* Canals (macho de Horco Molle, Tucumán; CZI): 9, oculario, vista posterior; 10, coxa, trocánter y base de fémur IV derechos, vista lateral. La escala representa 1 mm en Figs. 1, 2, 3, 7 y 10, y 0.5 mm en Figs. 4, 5, 6, 8 y 9.

III con una hilera posterior completa y un esbozo anterior irregular; áreas IV, V y tergitos libres, sendas filas de gránulos alargados, excepcionalmente en el área IV se agrega un rudimento de segunda hilera anterior; áreas laterales, una hilera de gránulos bajos, poco llamativos; opérculo anal, escasos gránulos en dos filas transversales; esternitos con una hilera de gránulos diminutos. Patas I a III

Tabla 1.—*Pachyloides hades* nueva especie: medidas en mm de holotipo y alotipo.

		Holotipo	Alotipo
Escudo	longitud	6.65	6.19
	ancho máximo	5.57	5.11
Pata I	long. total	11.89	10.61
	long. fémur	2.88	2.55
Pata II	long. total	17.03	15.39
	long. fémur	4.13	3.86
Pata III	long. total	15.13	13.56
	long. fémur	3.83	3.54
Pata IV	long. total	20.82	17.88
	trocánter	1.96	1.18
	fémur	4.58	4.26
	patela	2.10	1.77
	tibia	4.06	3.50
	metatarso	5.57	4.91
	tarso	2.55	2.26
Pedipalpos	long. total	7.83	7.56
	long. fémur	1.96	1.83
Quelíceros	long. total	2.03	2.10
Oculario	ancho	1.05	0.98
	alto	0.34	0.33

inermes, granulosas. Coxa IV con apófisis curva, dirigida hacia atrás, de extremos vueltos levemente hacia afuera; en norma dorsal, deja visible la articulación externa con el trocánter. Trocánter IV con apófisis lateral lobuliforme; sobre la articulación con el fémur, apófisis dorsal subcónica, alargada, dirigida hacia arriba; pequeña apófisis roma, ventromesial, en el margen posterior del artejo. Fémur IV suavemente curvado en vista lateral; superficie dorsal con hileras longitudinales de gránulos, destaca una hilera completa de gránulos perliformes en el borde dorsolateral; hilera mesial de apófisis subtriangulares, mayores hacia el ápice del artejo (en su extremo proximal son tubérculos bajos); hilera ventrolateral similar, de apófisis más pequeñas; hilera ventral de pocos tubérculos redondeados; tres apófisis apicales dorsales, la mesial es la mayor del artejo. Pene: glande con parte ventral subrectangular, alargada, con dos grupos de tres espinas en cada borde lateral, uno subterminal y uno basal; un pequeño tubérculo entre ambos grupos de espinas, otro próximo al grupo de espinas basal, y dos cercanos al grupo subterminal. Parte dorsal de base ancha, cuyos bordes, en vista dorsal, ocultan parcialmente las espinas basales; túbulo seminal con proceso ventral terminado en dos puntitas. *Hembra*: Escudo dorsal con gránulos más pequeños y escasos que en el macho. Patas I a III inermes. Coxa IV con una pequeña apófisis cónica lateral. Fémur IV: hileras longitudinales de gránulos, algo más destacados y aguzados en posición ventrolateral y ventromesial; apófisis apicomesial pequeña. Ovipositor: extremo apical tetralobado, con 10 espinas setiformes (tres espinas en los lóbulos dorsales, dos en los ventrales); en el alotipo se agrega una cuarta espina en el lóbulo dorsal derecho; vagina interna con cuatro pares de receptáculos seminales.

Comparación y diagnóstico.—La especie que más se aproxima a *Pachyloides hades* es *Pachyloides tucumanus*, presente también en la provincia de Tucumán pero a menor altitud, en ambientes de selva. Las principales diferencias consisten en la apófisis dorsal del trocánter IV del macho, que en *P. hades* termina en

Tabla 2.—Número de tarsitos en *Pachyloides hades* nueva especie; frecuencias halladas en el material estudiado.

	Número de tarsitos						<i>n</i>
	5	6	7	8	9	10	
Machos							
T I	3	37	—	—	—	—	40
T II	—	1	2	14	18	2	37
T III	2	1	37	—	—	—	40
T IV	—	1	33	3	—	—	37
Hembras							
T I	1	36	—	—	—	—	37
T II	—	—	2	22	15	—	39
T III	—	1	38	—	—	—	39
T IV	—	—	39	—	—	—	39

forma más aguzada (Figs. 3 y 10), y en la armadura del oculario (Figs. 4 y 9), mucho más desarrollada en *P. tucumanus*; por otra parte, el pene aparece en la nueva especie más deprimido en vista lateral. Otras diferencias, algo sutiles, afectan la armadura de coxa y fémur IV del macho, la granulación dorsal y el tamaño de los especímenes.

También *Pachyloides thorellii* Holmberg, especie cercana a *P. tucumanus*, muestra similitudes con *P. hades*. Cabe señalar que Ringuelet (1959) considera a *P. tucumanus* como subespecie de *thorellii*, criterio que no comparto; este autor supone que la provincia de Tucumán es la “zona de intergraduación” entre tales “razas geográficas”. Los hallazgos seguros de *P. thorellii*, sin embargo, se limitan a la provincia de Buenos Aires, Argentina, y al Uruguay. Los machos de esta especie se reconocen fácilmente pues la apófisis lateral del trocánter IV está reducida a un reborde esclerosado; la apófisis dorsal, en tanto, es idéntica a la de *P. tucumanus*, y permite la distinción con *P. hades*. Las hembras de *P. thorellii* poseen una pequeña apófisis dorsal en el trocánter IV (Canals 1943), ausente en los dos *Pachyloides* de Tucumán.

Pachyloides hades fue confundida con *Daguerreia maculata* Canals-simpátrida de *P. tucumanus*-, pero ésta es una especie claramente distinta, por su coloración oscura, gránulos dorsales muy conspicuos, y su peculiar armadura en fémur y, especialmente, trocánter IV del macho.

Material estudiado.—ARGENTINA: Provincia de TUCUMÁN; El Infiernillo, 5 abril 1986 (L. Acosta), holotipo macho y alotipo hembra (MACN 8620); iguales datos, 1 macho y 1 hembra paratipos (CZI); iguales datos, 7 machos, 5 hembras, 11 juv. (CZI); id. loc., 5 abril 1965 (W. Weyrauch), 2 machos (MLP); iguales datos, 1 macho, 2 hembras paratipos (IML s/n), “*Daguerreia maculata*” Ringuelet det. 1965; id. loc., 12 diciembre 1947 (R. Golbach), 3 machos (IML 00021); id. loc. y col., 28 noviembre 1947, 1 macho (IML 00019); id. loc. y fecha (O. Budin), 1 macho (IML 00020); La Quebradita, Tafí del Valle, 4 abril 1986 (L. Acosta), 1 macho y 1 hembra paratipos (MACN 8621); iguales datos, 2 machos, 6 hembras, 4 juv. (CZI); “Departamento Tafí”, sin especificar localidad, 21 octubre 1983 (Schocchi), 1 macho, 4 hembras, 1 juv. (IML s/n).

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SPIDERS OF SPANISH MOSS IN THE DELTA OF MISSISSIPPI

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ABSTRACT

Arthropods were collected monthly during a 13-month period from Spanish moss on water oak trees in Leroy Percy State Park, Washington County, Mississippi. Of the ca 2000 arthropods collected, spiders (600), beetles (600), chalcidoid wasps (500), and miscellaneous insects (300) represented the major groups. Peak population levels of spiders occurred in spring and fall, as did the occurrence of various crop pests. Spiders were represented by 13 families, 22 genera, and 29 species. Seventy percent of the total spider sample was composed of two species that breed in Spanish moss, *Metaphidippus tillandsiae* Kaston and *Anyphaena maculata* (Banks). Steadily declining non-spider arthropod populations in Spanish moss throughout the fall-winter-spring period suggest that the predatory activity of spiders may have an effect on over-wintering arthropod populations.

INTRODUCTION

Spanish moss (*Tillandsia usneoides* L.) (Bromeliaceae) is an epiphytic member of the Pineapple Family that forms long hanging tufts on branches of trees in damp or swampy areas and is distributed from Texas east to Florida and north to Virginia on the Coastal Plain (Fernald 1950). During the winter, this plant can be quite conspicuous on deciduous trees and locally abundant. During the course of a search of the potential overwintering habitats of the tarnished plant bug, *Lygus lineolaris* (Palisot) (Heteroptera: Miridae), samples from Spanish moss revealed a diverse fauna of arthropods. Spiders were the most abundant taxonomic order in the samples, and information is presented here on their seasonal composition, abundance, and potential impact on other arthropod inhabitants.

METHODS AND MATERIALS

Samples were collected from May 1985 through May 1986 at Leroy Percy (L.P.) State Park, Washington County, Mississippi. This park is a 1000 ha forest

surrounded by agricultural lands planted in rice, soybeans, and cotton. Early-successional habitats (e.g., oldfields and roadside margins) are abundant in the park and contain plants supporting populations of crop pests, particularly *Erigeron* spp. (Compositae) as a host of *Lygus lineolaris*. Approximately one-third m³ of Spanish moss was collected monthly (except November, due to flooding) from each of the same three water oak trees (*Quercus nigra* L.). These trees were located at the south end of a 10 ha mowed field of mixed grasses that was surrounded by low damp woods subject to periodic flooding. Each tree was at least 10 m from the border of the woods and 15 m from each other. Sampling was accomplished by standing on top of a truck cab under each tree, surrounding a clump of moss with a 1/3 m³ fine-mesh organdy bag, cutting off the tree branch at the bag opening, and continuing until the bag was full. The 3 bags were then placed in a large plastic bag and transported to the laboratory, frozen at -20° C for 12-36 hours, and then examined under magnification. Assistance with spider identifications was provided by G. B. Edwards and voucher specimens were deposited at Florida State Collection of Arthropods, Gainesville; Mississippi Entomological Museum, Mississippi State University, Starkville; and USDA-APHIS-PPQ-IFAS, Gulfport, Mississippi.

RESULTS AND DISCUSSION

Collections from Spanish moss over a 13-month period produced approximately 2000 arthropods. The majority of specimens were spiders (600), Coleoptera (600), and chalcidoid Hymenoptera (500), with various other insect groups totaling an additional 300. Crop pest species in the collections included the tarnished plant bug (3); chinch bug, *Blissus* sp. (3); flea beetle, *Altica* sp. (3); stink bug, *Euschistus* sp. (2); cereal leaf beetle, *Oulema* sp. (2); boll weevil, *Anthonomus* sp. (1); and bean beetle, *Cerotoma* sp. (1). These data indicate that, at least for the sites sampled, Spanish moss is not a significant refuge or breeding habitat for insects known to be pests on field crops. Predators and parasites of crop pests were present in low numbers and included *Coleomegilla* sp. and *Lebia* sp. (Coleoptera), *Orius* sp. and *Zelus* sp. (Hemiptera), *Chrysopa* sp. (Neuroptera), and *Micropletis* sp. (Hymenoptera).

Spiders were represented by 13 families, 22 genera, and 615 individuals (Table 1). Identification of immature spiders was particularly difficult and created some tabulation problems. All adult, and most penultimate, specimens were identified to species. Some immatures (e.g., *Metaphidippus tillandsiae* Kaston) could be identified without confusion. Some immatures [e.g., *Phidippus putnami* (Peckhams)] were captured in a silken retreat with an adult female and thus were identified by association. Some immatures [e.g., *Anyphaena maculata* (Banks)] were identified to genus, and the presence of adult specimens of only one species within the genus permitted a tentative species determination. When the adults of two species within a genus were present (e.g., *Philodromus*), the immatures could usually be associated with one of the species. Some immatures (e.g., *Clubionoides* sp.) could be identified to genus, but the absence of adult specimens prevented a species association. With these limitations, Table 1 lists 29 species, of which only 14 are represented by adult specimens. This list also contains 11 additions to the state list as compiled by Dorris (1972).

The abundance of spiders in Spanish moss was greatest in September and May with the appearance of large numbers of immatures and was at low levels in both mid-summer and late winter when adults predominated. The number of species was highest (12) in May and December and lowest (4) in July. Eighty-five percent of the total spider sample was composed of only four species. These four appeared to be the only species reproducing within Spanish moss and warrant further comment.

***Metaphidippus tillandsiae* Kaston.**—Two hundred forty-one specimens of this species were obtained, representing all sampling periods. Overwintering occurs in the adult stage, with an exclusively immature population in the summer and adults first appearing in October. This species was first described by Kaston in 1973 and has only been recorded from Spanish moss. The distribution of *M. tillandsiae* — North Carolina south to Florida, west to Louisiana — is entirely within the range of Spanish moss (Fernald 1950; Kaston 1973). It is probable that this species is restricted to Spanish moss and may be a major predator within that microhabitat.

***Anyphaena maculata* (Banks).**—One hundred eighty-six specimens were obtained, representing all sampling periods except January. Overwintering occurs in both adult and immature stages, with an exclusively immature population in the summer and adults first appearing in October. This species was redescribed in 1974 and has been recorded from Spanish moss, sweeping in bottomland pine and hardwood forests, sifting of leaf litter, and malaise trap (Platnick 1974), as well as from cotton (Whitcomb and Bell 1964). The distribution of *A. maculata* — New York south to Georgia, west to Illinois and Louisiana — is considerably broader than Spanish moss (Platnick 1974), and thus is not restricted to this microhabitat. This predator, combined with *M. tillandsiae*, may exert a dominant influence on the abundance of arthropods in Spanish moss at the L.P. State Park sites.

***Philodromus keyserlingi* Marx.**—Fifty-three specimens were obtained, representing all sampling periods except June. Overwintering occurs in the immature stages, with adults only present in May. This species was redescribed in 1961 and has been recorded from wasp's nests (Dondale 1961), as well as from corn (Plagens 1985), peanuts ((Agnew et al. 1985), cotton (Skinner 1974), and soybeans (LeSar and Unzicker 1978). The distribution of *P. keyserlingi* is very broad, occurring from Massachusetts south to Florida, west to Iowa and New Mexico (Dondale 1961). The temporal pattern of occurrence in the L.P. State Park samples, combined with the published records of geographic and habitat distribution, suggests that this species is an occasional vagrant and facultative breeder in Spanish moss.

***Nodocion floridanus* (Banks).**—Forty-four specimens were obtained, representing all sampling periods except July, January, and February. Overwintering may occur in both the adult and immature stages, but the absence of specimens in January and February precludes a definite determination. Adults were present only in May and June, the same pattern of occurrence as reported from Arkansas cotton and pine (Heiss and Allen 1986). This species was redescribed in 1980 and has been reported from houses, wasp's nests, under bark, on pine trees, in bowers and nests (Platnick and Shadab 1980), as well as from cotton (Dean et al. 1982). The distribution of *N. floridanus* is also very broad, occurring from Massachusetts south to Florida, west to Minnesota and Arizona. (Platnick and

Table 1.—Spiders of Spanish moss at Leroy Percy State Park, Mississippi, 1985-1986. Explanation of symbols: M = male, F = female, PM = penultimate male, PF = penultimate female, IM = immature (juvenile). * = no sample.

Taxon	Instar	M	J	J	A	S	O	N	D	J	F	M	A	M	Total
ANYPHAENIDAE															
<i>Anyphaena maculata</i> (Banks)	M	1							3		1				5
	F						3		5		6	1	2	3	20
	PM					3	1							1	5
	PF					2									2
	IM	4	6	10	6	26	10		10		3		2	77	154
<i>Teudis mordax</i> (O.P.-Camb.)	M	2	1											1	4
	IM	1											1		2
ARANEIDAE															
<i>Eustala cepina</i> (Walck.)	M													1	1
<i>Neoscona hentzi</i> (Keys.)	F					1									1
<i>N. domiciliorum</i> (Hentz)	F			1											1
CLUBINONIDAE															
<i>Clubionoides</i> sp.	IM										10				10
DICTYNIDAE															
<i>Dictyna</i> sp.	IM									1					1
GNAPHOSIDAE															
<i>Cesonia bilineata</i> (Hentz)	IM												1		1
<i>Nodocion floridanus</i> (Banks)	M	1												1	2
	F		1											3	4
	PM											1			1
	PF	1							1						2
	IM	2	1		1	8	1		2			2	14	7	38
LINYPHIIDAE															
<i>Ceraticelus</i> sp.	PM								2						2
	PF												1		1
	IM								1	1				2	4
LYCOSIDAE															
<i>Pardosa</i> sp.	IM								2	1					3
MIMETIDAE															
<i>Mimetus</i> sp.	IM								1						1
PHILODROMIDAE															
<i>Philodromus keyserlingi</i> Marx	M	2													2
	F													1	1
	PM													2	2
	IM	1		1	1	3	4		20	5	8	1	1	3	48
<i>P. vulgaris</i> (Hentz)	F													1	1
PISAURIDAE															
<i>Pisaurina</i> sp.	IM					1									1
SALTICIDAE															
<i>Eris militaris</i> (Hentz)	M											1		1	2
<i>Hentzia</i> sp.	IM									1		1			2
<i>H. mitrata</i> (Hentz)	M									1					1
<i>Metaphidippus</i> sp.	IM										1				1
<i>M. tillandsiae</i> Kaston	M						14		14	14	11	7	4	2	66
	F	1					15		22	9	13	6	3	9	78
	PM					8									8
	IM	4	12	21	10	30	11				1				89
<i>Phidippus</i> sp.	IM										1				1
<i>P. putnami</i> (Peckhams)	M								1						1
	F					1									1
<i>Platycryptus undatus</i> (DeG.)	IM					25									25
	IM								1						1

<i>Zygoballus</i> sp.	IM								1			1		2	
<i>Z. nervosus</i> (Peckhams)	M								1					1	
THERIDIIDAE															
<i>Euryopis</i> sp.	IM										1			1	
<i>E. funebris</i> (Hentz)	M												2	2	
<i>Theridion</i> sp.	IM		1		1		1		1					4	
THOMISIDAE															
<i>Misumenops</i> sp.	IM								6	2	1			9	
TOTALS	No. Individuals	20	22	33	19	108	60	*	94	36	56	20	30	117	615
	No. Species	5	5	4	5	7	5	*	12	7	8	6	8	12	29

Shadab 1980). This species is probably a facultative breeder in Spanish moss, with individuals moving in and out of the microhabitat at various times of the year.

Seventy-five years ago Rosenfeld (1911, 1912) published his Louisiana investigations on the use of Spanish moss as an over-wintering habitat by the boll weevil and its associated predators and competitors. From 12 samples (197 lbs) collected in December, January, and June, he obtained 2614 insects and 287 spiders. The dominant insect was an aphid ant (*Cremastogaster* sp.), with 1481 individuals. Of the remaining insects, 343 (30.3%) were *Anthonomus* weevils and 25 (2.2%) were *Nezara* stink-bugs, with most of the rest beneficials such as coccinellids and nabids. After noting the small number of insects obtained in June, he concluded that Spanish moss "is much sought after by a large number of insects as hibernating quarters".

In 1930 and 1931, Rainwater (1941) collected Spanish moss from trees adjacent to cotton fields in Louisiana and identified 139 insect species. Both the boll weevil and the tarnished plant bug were present during late fall to early spring and apparently "enter hibernation and survive the winter in this material". Although "numerous spiders were present", Rainwater did not collect and identify them.

Based on the 1985-1986 collections, statements from Rosenfeld and Rainwater may be broadened to indicate that arthropod populations in Spanish moss can be both large and diverse at all times of the year. It may also be significant that a relatively greater proportion of the arthropod population in the 1985-1986 samples was composed of spiders (predators), relative to the 1911-1912 samples. This factor alone may be sufficient to account for the lower numbers of crop pests in the 1985-1986 samples, though the relative proximity of cotton and the number of trees sampled could also be important.

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A TEST OF THE MECHANICAL ISOLATION HYPOTHESIS IN TWO SIMILAR SPIDER SPECIES

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ABSTRACT

External reproductive organs of spiders are often species-specific and are important taxonomic characters in species identification. One explanation of this is the mechanical isolation or lock-and-key hypothesis. It predicts that in closely related species with overlapping ranges, morphological character displacement should occur in regions of sympatry to prevent costly interspecific copulation attempts. To test this hypothesis, we measured homologous external genital sclerites of male *Larinioides (Nuctenea) scolopetaria* and *L. patagiata* (Araneidae) and statistically compared their means and variances for sympatric and allopatric regions of their distribution. Differences in both mean and variance were observed, but the number of sclerites that differed between regions of sympatry and allopatry was not greater than the number that differed between adjacent regions of sympatry. Thus, these species failed to demonstrate the character displacement predicted by the mechanical isolation hypothesis.

INTRODUCTION

In spiders, as in many invertebrate groups, genitalic differences have been widely used to distinguish species. The "lock-and-key" mechanism of reproductive isolation has traditionally been used to explain these differences in the sclerotized, external genitalia of both male and female spiders. It postulates that the genitalia are specifically shaped so that during mating they couple correctly only between conspecifics (Mayr 1963). Although this hypothesis is commonly used to explain the often small genitalic differences which separate species, it has never been put to a critical test. Grasshoff's (1973a, b, 1975) descriptions of the mechanisms that couple male and female genitalia make it plausible that small differences in one or several genitalic parts (sclerites) could preclude mating between related species. However, for most species the precise functions of genitalic sclerites are unknown and the amount of difference sufficient to prevent successful mating is unclear. Additionally, only Coyle (1985) has quantified the genitalic variation in a

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population of spiders and no study has analyzed the pattern of variation over a species' range.

Eberhard (1985) raises several objections to the traditional lock-and-key or mechanical exclusion mechanism, the first being that it was originally proposed for insects in which the female genitalia are relatively rigid, whereas the genitalia in many other groups are not rigid and, therefore, probably incapable of mechanical exclusion. Another objection is that species-specific sclerites of the male genitalia of some species contact parts of the female genitalia that do not differ among species, a situation inconsistent with the lock-and-key explanation. A strong theoretical objection to the mechanical isolation hypothesis is that selection should favor females that can identify a potential mate's species early in courtship (prior to physical contact), since courtship and copulation are costly for a female (Daly 1978).

As alternatives to the lock-and-key mechanism, Eberhard (1985) suggests four hypotheses to explain the often species-specific nature of animal genitalia: (1) species isolation by genitalic stimuli, (2) pleiotropic effects of alleles selected in other contexts, (3) mechanical "conflict of interest" between males and females, and (4) sexual selection by female choice. Eberhard's evidence more strongly supports the latter hypothesis.

The objective of this study is to evaluate the mechanical isolation hypothesis for species-specific genitalic differences by testing two of its predictions. If, as this hypothesis predicts, genitalic differences prevent costly and potentially dangerous interspecific copulation attempts between closely related species, then genitalic features of partially sympatric species should show greater differences in regions of sympatry than in regions of allopatry. Additionally, if two species with similar genitalia are influenced by interspecific competition for mates, their genitalia should be less variable within areas of sympatry than within areas of allopatry. To test these predictions we measured and compared homologous genitalic structures of two similar spider species.

MATERIALS AND METHODS

Criteria for selecting study species.—Before selecting study species, we established four requirements. First, the species' taxonomy must have been recently revised to insure that they are valid morphological species and to provide a current picture of their distribution. Second, the species must have similar genitalic structures and occur in areas of sympatry and allopatry only with one another, or both their ranges must be completely sympatric with one or more closely related species. This is necessary to insure that any detected effects do not result from interaction between a third species and only one of the two study species. Third, species must have sufficient size and seasonal overlap to make interbreeding a real possibility. Fourth, an ample number of museum specimens must be available for study.

Surprisingly few spider species meet all of these requirements; however, two species of Araneidae, *Larinioides sclopetaria* (Clerck) and *Larinioides patagiata* (Clerck), qualify, the systematics of their genus having been recently revised by Levi (1974). Subsequently, Grasshoff (1983) transferred these and two other species from *Nuctenea* to *Larinioides* Caporiacco 1934. Although both species are

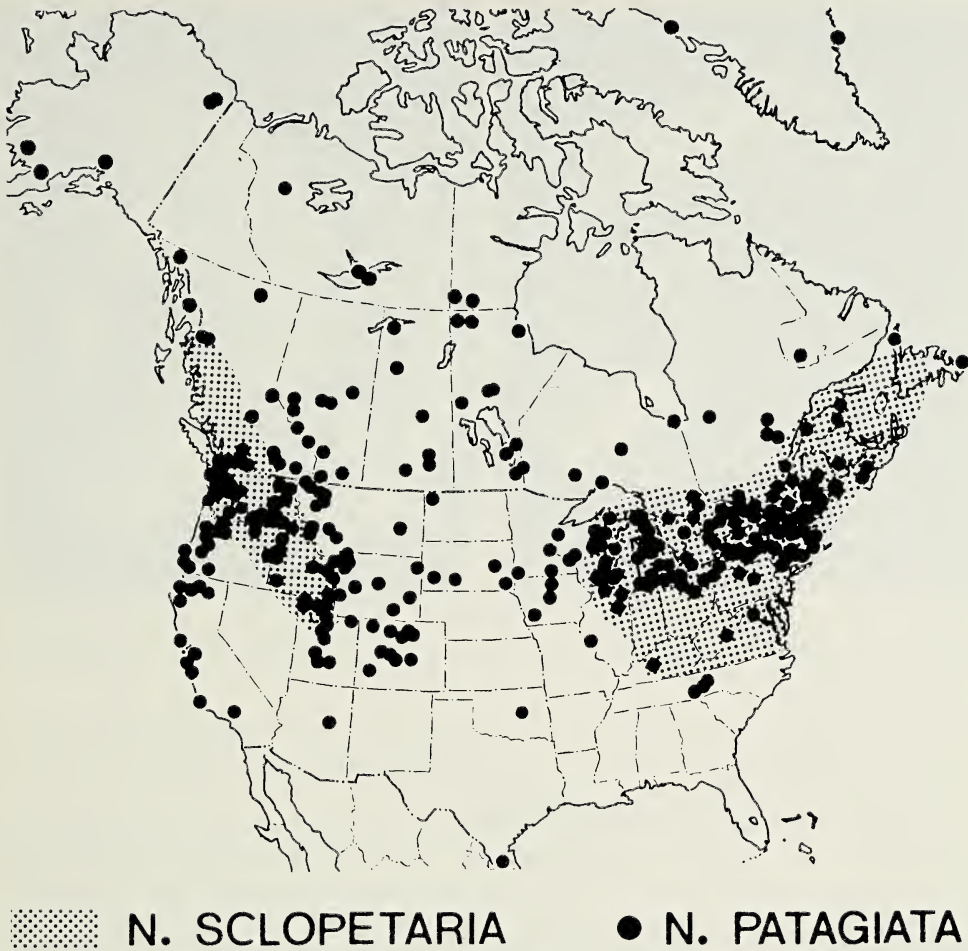


Figure 1.—Ranges of *Larinioides sclopetaria* and *Larinioides patagiata*, modified from Levi (1974).

found in Eurasia, this study focuses only on the specimens collected in North America. Here, the ranges of both species are completely encompassed by that of *Larinioides cornuta* (Clerck). *Larinioides sclopetaria* and *L. patagiata* have regions of sympatry on both the east and west coasts and an area of allopatry for *L. patagiata* between (Fig. 1).

Both the sizes and times of maturation of these two species overlap. *Larinioides sclopetaria* males have a carapace length of 3.7–4.2 mm and females a carapace length of 3.9–4.3 mm; *L. patagiata* has size ranges of 2.9–3.8 mm and 2.5–4.0 mm, respectively (Levi 1974). Size overlap can also be documented in specific sympatric regions (blocks A–D, Fig. 4) of each species range. Within each region, the smallest *L. patagiata* males had palpal femur and cymbium lengths that were 0.8–1.0 times those of the smallest *L. sclopetaria* males and the largest *L. patagiata* males had values that were 0.44–0.80 times those of the largest *L. sclopetaria* males.

These two species show no evidence of temporal isolation. In Connecticut, mature *L. sclopetaria* and *L. patagiata* can be found throughout the year (Kaston 1948). *Larinioides sclopetaria* is more commonly found around buildings than is *L. patagiata*, although Kaston (1948) notes that the former species is also found



Figure 2.—Scanning electron micrographs of *Larinioides scolopetaria* (A) and *Larinioides patagiata* (B) left male pedipalps in ventral view. TA = terminal apophysis, C = conductor, CY = cymbium, E = embolus, MA = median apophysis. Scale bars each represent 200 μ m.

on bushes and rocks near streams. This observation could suggest either that *L. scolopetaria* has a greater tolerance or is a more opportunistic species or that it prefers a different habitat than *L. patagiata*.

Distributional history.—Although both *L. scolopetaria* and *L. patagiata* are sympatric in Europe, Levi (1974) suggests that, due to its frequent association with man-made structures, *L. scolopetaria* may have been introduced into North America (*L. patagiata*'s native status is unquestioned). However, he also notes that in Europe *L. scolopetaria* is also most commonly found on buildings. To evaluate this species' distributional history, we employed methods similar to those used by Nyffeler et al. (1985). This involved examining and plotting the collecting localities and dates of museum specimens of both species to determine if there was convincing evidence for the range expansion of *L. scolopetaria*.

Measurements.—Sclerite measurements were taken at 50X using a dissecting stereo microscope fitted with an ocular micrometer scale. Values were recorded to the nearest half unit, providing a resolution of 10 μ m. Only measurements of sclerites which could be positioned consistently and had well defined boundaries were used. In order to determine which palpal indexes could be accurately taken, three duplicate sets of preliminary measurements were taken on five males of the same species over a period of ten days.

Four types of measurements were used in this preliminary study: overall spider size (carapace length and first femur length), overall palp size (cymbium height and width), sclerite dimensions, and distances separating one sclerite from another. Coefficients of variation for all repeated measurements of the same species except the latter were less than 0.13, indicating that only sclerite separation could not be consistently measured.

In males of both species, one measurement (first femur length) of spider size and 16 palpal measurements were taken. First femur length (FFL) was measured

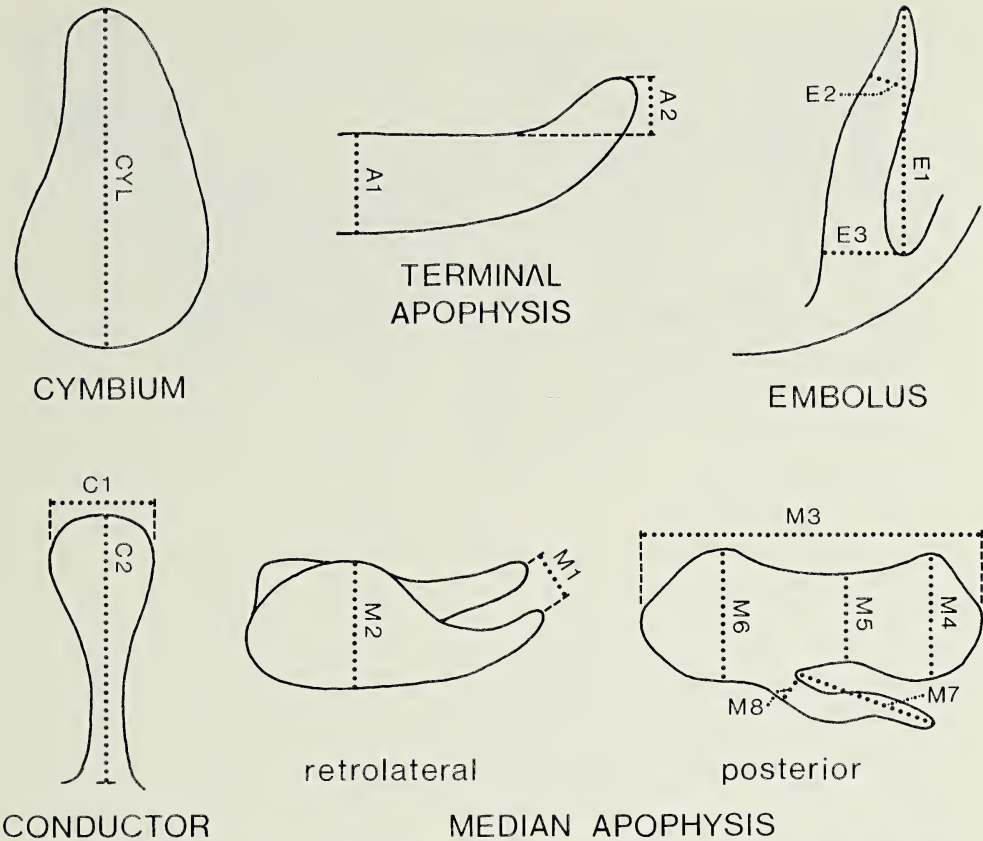


Figure 3.—Male palpal sclerites (not to scale), as oriented for measurement, and the features measured.

retrolaterally with the leg oriented perpendicular to the axis of measurement. Palpal characters (Figs. 2 and 3) were measured on the left pedipalp after it was removed from the body (unless the right pedipalp had been removed by a previous examiner). For the following palpal measurements, the dimensions being measured were oriented perpendicular to the axis of observation (directions refer to palpal orientation): cymbium length (CYL), prolateral view; palpal femur length (PFL), prolateral view; conductor width (C1) and length (C2), retrolateral view; terminal apophysis width (A1), apical (anterior) slightly retrolateral view (In *L. sclopetaria*, the greatest width measurement was taken; in *L. patagiata*, width was measured where the edges of the apophysis become parallel to one another.); curvature of the terminal apophysis (A2 - the distance from the main body beyond which the curved end projected), apical and slightly retrolateral view; embolus length (E1 - from the tip to the point where the base was curved on itself), anterior third width (E2), and basal width (E3), prolateral and ventral views, perpendicular to axis of measurement in an anterior-posterior direction and rotated laterally until the point where the base curved back on itself began to be eclipsed; median apophysis projection separation (M1) and depth (M2), prolateral and perpendicular to the axis of measurement in a lateral direction, rotated anterior-posteriorly until the main body just covered the upper edge of the bottom projection; median apophysis length (M3), upper ¼ width (M4),

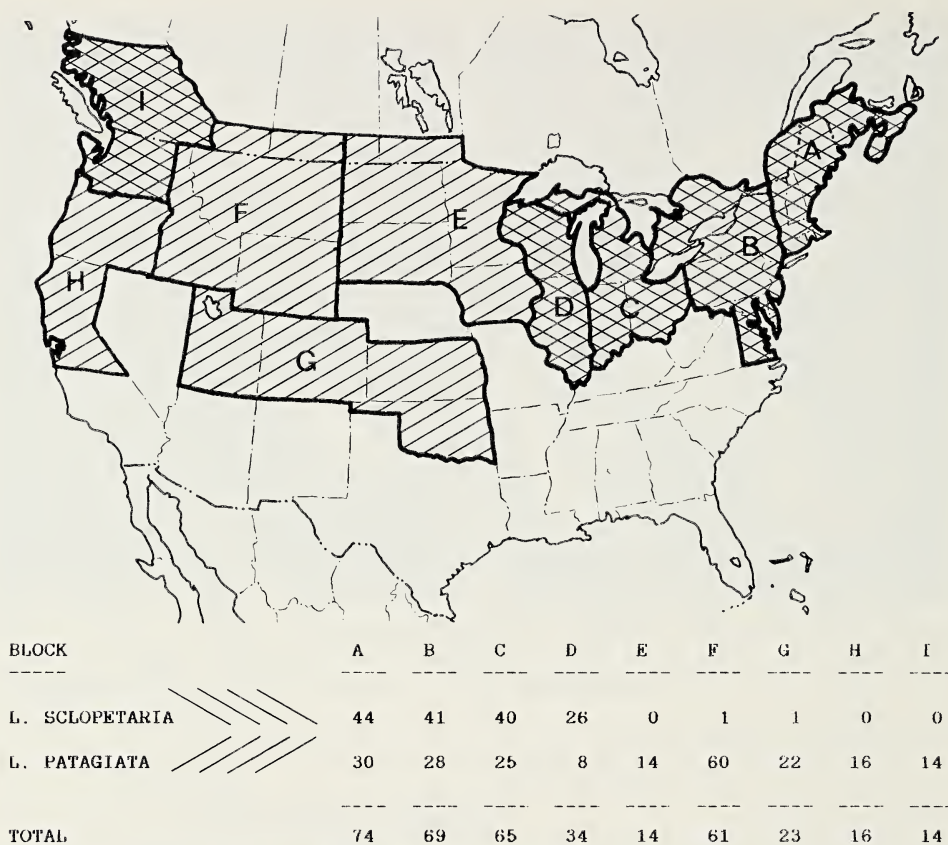


Figure 4.—Range “blocks” and the number of specimens from each.

central width (M5), basal width (M6), and projection length (M7) and width (M8), posterior and slightly ventral, then rotated until the gap between the two projections and the main body was just barely eclipsed.

All statistical tests on these measurements were performed using SAS V (SAS Institute, Inc., SAS Circle, PO Box 8000, Cary, NC, 27511-8000).

Establishing range blocks.—Using state lines as boundaries, species ranges were divided into subunits (blocks) shown in Fig. 4. These blocks had similar areas and, except for the western blocks of *L. sclopetaria*, were represented by sufficient museum specimens to permit statistical tests. The scarcity of western *L. sclopetaria* males (Fig. 4) does not preclude comparisons of *L. patagiata* in areas of allopatry and sympatry with *L. sclopetaria*, as established by female specimens of the latter species.

Preliminary tests.—Before comparative statistical tests were performed, three preliminary steps were necessary. First, the normality of all measurements was tested with the Kolmogorov goodness-of-fit test to assure that assumptions of the statistical tests were met. Second, discriminate analysis was used to determine how well specimens of each species could be assigned to the correct geographical block. Only if most of the specimens from a block can be assigned to that block on the basis of palpal features alone, are the proposed blocks appropriate for this study. Third, *F*-tests comparing variability between the population and state levels, and the state and block levels were performed to determine if, as

hypothesized, variability was greater in more inclusive units. If this is found to be correct, it means that blocks can be analyzed without being biased by overly large population or state variation.

Test of clinal variation.—We examined geographic variation because the patterns of variation within a species must be understood in order to avoid the problem of interpreting clinal variation as support for the mechanical isolation hypothesis. A large difference in mean measurement values between regions of sympatry and allopatry could actually be due to clinal variation, rather than the effect of range overlap.

To reveal less conspicuous, but congruent patterns in sclerite size differences indicative of clinal variation, we calculated sclerite measurement means for each geographic block (Fig. 4). For *L. patagiata*, this created a matrix of nine rows (blocks) and fifteen columns (one for each sclerite measurement except those measuring overall size - FFL, CYL, PFL) and for *L. sclopetaria*, a matrix of four blocks (the other two blocks included only one specimen each and were excluded from this analysis) and fifteen sclerites was constructed. From this matrix, we determined the number of sclerites for which each block had the highest value, the next highest value, etc., until the ninth lowest position was reached. These ranking variables were compiled into a summary table and from these, consensus rankings (Table 3) for each species were derived. These rankings were designed to detect any continuous trends in mean sclerite measurements across the ranges of the two species. If sclerite measurements show east-west or north-south clinal variation, consensus rankings will order the blocks of each species into a logical, east-west or north-south geographical sequence. However, this approach is not likely to detect other patterns, such as changes in sclerite values from the center of a species' range to its periphery or regional differences due to altitude or precipitation differences.

Test of character displacement.—We evaluated evidence for character displacement by comparing the means and variances of adjacent geographic blocks using *t*-tests and *F*-tests, respectively. When variances differed significantly ($P < 0.05$), *t*-tests for unequal variances were used.

RESULTS

Preliminary tests.—The Kolmogorov goodness-of-fit test shows the data to be normally distributed ($P \leq 0.05$). Discriminate analysis of block divisions (Table 1) shows a high percentage of specimens correctly identified, indicating that, although arbitrary, these block divisions are appropriate ones for pooling the data. Tests of variability between populations and states, and states and blocks showed that variability was significantly greater ($P < 0.05$) in more inclusive units.

Distributional history.—Museum specimens of both *L. sclopetaria* and *L. patagiata* date to the 1860's. Nothing about the pattern of acquisition of additional specimens chronicles an expanding range for either species. Specimens of both species collected in the eastern United States and Canada between 1864 and 1885 fully occupy the present-day eastern range of *L. sclopetaria* (Fig. 5). Those added during the next two decades simply increase the density of points within this range (Fig. 5), and do not, as Nyffeler, et al. (1986) found for the

Table 1.—Discriminant analysis of palpal features among geographic blocks. Letters in parentheses refer to those blocks into which the most frequently misidentified specimens were placed.

Species	Block	No.	% Identified correctly	Highest % identified incorrectly
<i>L. sclopetaria</i>	A	44	75	14 (B)
	B	41	90	5 (A & C)
	C	40	73	12 (A)
	D	26	92	4 (A & B)
<i>L. patagiata</i>	A	30	77	13 (E)
	B	28	86	11 (D)
	C	25	92	4 (D & E)
	D	8	100	0
	E	14	79	21 (D)
	F	60	75	7 (B & G)
	G	22	90	5 (E & F)
	H	16	88	12 (E)
	I	14	100	0

introduced species, *Steatoda bipunctata* (L.); depict a range expansion from the Northeastern coast of the United States inland and along the St. Lawrence River. Likewise, the number of new specimens of each species added to museum collections and the number of new state records resulting from this increase (Table 2) does not portray the expansion of *L. sclopetaria*. In fact, these data suggest that it is *L. patagiata* whose range expanded, a misconception explained by an increase in the number of specimens collected from the western states.

Test of clinal variation.—For each species, the consensus ranking (Table 3) lists in order the block that has the greatest number of sclerites placing it in the first, second, third, etc. position. The percentage of sclerites which contributed to the ranking of blocks was never much greater than 50% and averaged about 39%, indicating that no strong consensus appeared in the ranking. Additionally, the resulting consensus ranking shows no consistent trends of east-west or north-south clinal variation in either species.

Test of character displacement.—Significant intraspecific differences in the means of 0-8 palpal sclerite measurements were observed between adjacent blocks of both *L. sclopetaria* and *L. patagiata* (Tables 4 and 5). However, the pattern of sclerites that differed changed from block to block. In the eastern United States



Figure 5.—Early distributional records for *Larinioides patagiata* and *Larinioides sclopetaria*.

Table 2.—A historical summary of the number of new specimens and new state records of *Larinioides patagiata* and *Larinioides sclopetaria*.

Time period	Number of specimens		Number of new state records	
	<i>L. patagiata</i>	<i>L. sclopetaria</i>	<i>L. patagiata</i>	<i>L. sclopetaria</i>
1864-1875	7	4 (36%)	(3)	(2) (40%)
1876-1885	12	9 (43%)	2	3 (60%)
1886-1895	0	5 (100%)	0	0 —
1896-1905	19	4 (17%)	4	3 (43%)
1906-1915	21	24 (53%)	4	2 (33%)
1916-1925	16	5 (23%)	5	1 (17%)
1926-1935	147	18 (11%)	9	2 (18%)
1936-1945	201	17 (8%)	6	0 (0%)
1946-1955	183	14 (7%)	3	0 (0%)
1956-1965	96	3 (3%)	3	1 (25%)
1966-1975	39	19 (33%)	0	3 (100%)

only M4, the median apophysis's upper width, differed significantly ($P < 0.05$) between blocks D and E of *L. patagiata* where the lock-and-key mechanism predicts the greatest difference. In contrast, in blocks A through D where *L. patagiata* and *L. sclopetaria* are sympatric, 1-6 *L. patagiata* sclerites differ significantly between adjacent blocks. A significant overall *L. patagiata* size (FFL) difference appears only between blocks A and B, indicating that the interpretation of these results is not confounded by interblock differences in spider size.

The lock-and-key mechanism predicts that in the West the means of more *L. patagiata* sclerites should differ between block I, which this species shares with *L. sclopetaria*, and adjacent allopatric blocks F and H than between blocks E-H where *L. patagiata* alone is found (Fig. 4). Table 5 shows that this is not the case. In *L. patagiata*, only A2, the terminal apophysis' distal curvature, differs significantly ($P < 0.05$) between blocks I and F and none of its sclerites differ

Table 3.—Consensus ranking of geographic blocks. This table lists in order the block that has the greatest number of sclerites placing it in the first, second, third, etc. position.

Species	Rank	Block	% of Sclerites contributing to block rank
<i>L. patagiata</i>	1	G	53
	2	F, I	20
	3	F, H	33
	4	A, F, H	27
	5	A	33
	6	C	47
	7	B	40
	8	B, D	27
	9	E	40
<i>L. sclopetaria</i>	1	A	53
	2	A, D	33
	3	B	47
	4	C	67

Table 4.—Male *Larinioides sclopetaria* first femur and palpal sclerite means (in μm) and (standard deviations) by geographical block. A “*” appears between blocks whose means differ significantly ($p \leq 0.05$) and a “+” between blocks whose variances differ significantly ($p \leq 0.05$). Blocks F and G were each represented by only a single specimen.

	BLOCK								
Feature	A		B		C		D	F	G
FFL	5852	+	5802	*	5418	*	6024	7470	7802
	(989)		(689)		(739)		(873)		
CYL	1413	+	1325	+	1300	+	1348	1640	1640
	(341)		(181)		(72)		(133)		
C1	253		248	+	238	*	252	300	280
	(19)		(16)		(26)		(23)		
C2	514	+	511	*	480		499	590	600
	(59)		(41)		(48)		(66)		
A1	185	+	180	+	186		187	240	200
	(24)		(17)		(23)		(20)		
A2	52	*	43		48		53	40	100
	(21)		(16)		(18)		(22)		
E1	328	+ *	314	+	305	*	321	380	400
	(35)		(17)		(31)		(27)		
E2	108	+ *	99	+	102	*	111	120	120
	(19)		(10)		(15)		(14)		
E3	135	*	121	+ *	143		145	120	140
	(15)		(14)		(25)		(21)		
M1	131	*	125		124		130	140	120
	(13)		(12)		(14)		(14)		
M2	242	*	232		230	*	243	260	260
	(19)		(19)		(24)		(18)		
M3	623	+	608		606		623	740	680
	(49)		(35)		(44)		(56)		
M4	241		236		229	*	243	240	240
	(26)		(24)		(26)		(26)		
M5	220		214		212		216	230	220
	(19)		(14)		(18)		(22)		
M6	306		313		306		305	320	300
	(31)		(24)		(24)		(28)		
M7	229		226	*	204	*	223	280	280
	(32)		(30)		(33)		(37)		
M8	73		71		66		70	80	100
	(12)		(13)		(15)		(16)		
PFL	804		782		766		816	1000	1000
	(86)		(73)		(92)		(113)		

significantly between blocks I and H. In contrast, 3-8 sclerites differ significantly between allopatric blocks E-H.

Likewise, intraspecific differences in variances do not support predictions of the lock-and-key mechanism that greater variance should be permitted in allopatric than sympatric regions. The variances of 1-4 (mean 2.3) *L. patagiata* sclerites differs significantly ($P < 0.05$) between adjacent allopatric blocks A-D, as compared with 1-4 (mean = 2.5) that differ between adjacent sympatric blocks E-H (Table 5). The variance of only two sclerites differs significantly between sympatric block D and block E, where *L. patagiata* alone is found. In the West, the variances of 0-2 *L. patagiata* sclerites differs between sympatric block I and adjacent allopatric blocks F and H. None of these observations lends support to the lock-and-key mechanism.

Table 5.—Male *Larinioides patagiata* first femur and palpal sclerite means (in μm) and (standard deviations) by geographical block. A “*” appears between the blocks whose means differ significantly ($p < 0.05$) and a “+” between the blocks whose variances differ significantly ($p < 0.05$).

Feature	BLOCK										
	A	B	C	D	E	F	G	H	I	F&H	F&I
FFL	4000 (333)	* 3666 (336)	3745 (480)	3920 (263)	3676 (321)	3689 (377)	3799 (364)	3577 (358)	3640 (389)	—	—
CYL	1335 (85)	* 1244 (76)	1251 (89)	1285 (99)	1214 (128)	+ * 1348 (86)	+ * 1422 (130)	* 1341 (104)	1341 (127)	—	+
C1	196 (20)	* 183 (21)	186 (26)	180 (15)	184 (23)	* 213 (21)	216 (26)	208 (18)	216 (19)	—	—
C2	535 (42)	* 507 (41)	511 (42)	505 (54)	495 (52)	* 548 (55)	566 (59)	+ * 525 (35)	542 (40)	+ *	—
A1	159 (31)	+ * 140 (19)	+ 146 (31)	139 (24)	149 (19)	145 (26)	147 (33)	146 (21)	135 (18)	—	—
A2	28 (13)	* 21 (9)	23 (11)	+ 50 (62)	+ 19 (10)	23 (12)	24 (14)	+ 21 (7)	19 (5)	+	+ *
E1	310 (31)	299 (34)	304 (23)	287 (35)	304 (28)	* 338 (31)	354 (43)	347 (28)	339 (31)	—	—
E2	86 (12)	82 (12)	83 (11)	76 (7)	78 (12)	* 92 (12)	93 (16)	89 (13)	94 (14)	—	—
E3	100 (20)	+ 93 (14)	* 105 (12)	97 (17)	87 (12)	* 102 (14)	+ 108 (24)	+ 106 (14)	101 (12)	—	—
M1	212 (28)	206 (20)	203 (26)	210 (28)	197 (37)	* 218 (30)	* 246 (25)	* 216 (24)	208 (20)	—	—
M2	236 (34)	226 (37)	213 (32)	* 242 (25)	219 (30)	229 (29)	234 (28)	* 209 (29)	213 (31)	*	—
M3	481 (69)	+ 469 (30)	480 (36)	492 (32)	447 (60)	+ * 506 (70)	506 (40)	485 (53)	504 (52)	—	—
M4	186 (24)	177 (29)	171 (26)	* 199 (22)	* 177 (20)	* 176 (29)	* 193 (28)	199 (37)	186 (25)	*	—
M5	335 (35)	* 306 (31)	318 (30)	+ 315 (60)	+ 321 (32)	334 (50)	348 (56)	+ 340 (29)	320 (28)	+	+
M6	272 (29)	265 (38)	278 (39)	275 (45)	253 (34)	* 283 (38)	287 (39)	290 (24)	287 (32)	—	—
M7	492 (90)	+ 479 (49)	466 (57)	471 (70)	461 (53)	* 513 (51)	527 (51)	524 (59)	529 (38)	—	—
M8	72 (21)	* 94 (22)	80 (28)	74 (19)	77 (39)	+ 97 (26)	93 (30)	97 (19)	101 (19)	—	—
PFL	697 (51)	* 626 (55)	653 (64)	676 (38)	638 (64)	673 (57)	+ 711 (83)	* 644 (64)	673 (77)	—	—

DISCUSSION

In the absence of a clearer understanding of palpal sclerite function, the mechanical isolating hypotheses predicts that, when adjacent blocks of a species range are compared, a greater number of sclerites should differ between a sympatric and an allopatric block than between two sympatric blocks. By failing to show this difference, this study fails to demonstrate the character displacement predicted by the lock-and-key mechanism. Even between sympatric blocks, there is a shift in the sclerites whose means differ significantly, making it difficult to argue that those *L. patagiata* sclerites that differ between regions of sympatry and allopatry (blocks D and E and blocks I and either F or H) are of greater importance in species isolation.

There are several levels of sclerite function: general orientation, alignment, and physical coupling. The last of these has the greatest potential to function in reproductive isolation. Since the exact function of several of the sclerites is unknown, we made an effort not to weight any sclerite beyond the limits of our ability to measure it consistently. Additionally, several measurements were taken on each sclerite to avoid neglecting any feature which might play a role in the actual coupling of the palp with the female's epigynum. Considering the large number of measurements taken from each specimen, a number of parameters involved in palp coupling were almost certainly analyzed. Two of the structures measured (the embolus and the conductor) are known to be directly involved in coupling (Grasshoff 1973a, b; Shear 1967). Therefore, the failure of this study to find evidence for character displacement cannot be dismissed on the grounds that it analyzes structures not involved in the coupling process.

This study emphasizes the danger inherent in establishing subspecies on the basis of differences in a few characters. Although blocks were established as arbitrary units for purposes of evaluating clinal variation, each meets the traditional definition of a subspecies as: "an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species" (Mayr 1963). As spiders are not known to respect state boundaries, it is likely that these two species' ranges could be divided into other arbitrary units, each distinguished by significant differences in one or more sclerites.

The use of museum specimens resulted in data from different localities and dates being compiled into a single set. There are no assurances that specimens found sympatrically at the species level are actually sympatric at the more important population level. However, most of the collectors were not interested specifically in one or the other of these large, conspicuous species and both species probably had an equal chance of being collected if they occurred in the same area.

Several problems are encountered in studies of character displacement (Grant 1972), the first being clinal variation. Some studies that have claimed to show character displacement (e.g., Brown and Wilson 1956; Ficken et al. 1968) have later been refuted because the morphological changes attributed to character displacement could be explained by clinal variation (Grant 1972). Although this study detected no north-south or east-west clinal variation in either species, the block design it employs is not well suited to detect changes in sclerite values due to local differences in such factors as altitude or precipitation. However, because these local differences have a limited influence on a block's values, they are less likely to compromise the design of our study.

A second potential difficulty is that the historical events responsible for the present distribution of most species are not well documented. If two species evolved in isolation and then came into contact, there would be opportunity for character displacement to occur. If they first originated sympatrically and then one vacated part of the other's range, there would be opportunity for character release to occur in the vacated region. Two facts suggest that the present-day distributions of the species studied have existed long enough to permit their palpal sclerites to respond to such increased or relaxed selection pressure. First, as early as the 1860's both species' eastern ranges appear fully occupied (Fig. 5). Second, between adjacent blocks of each species (except F and G of *L.*

sclopetaria that were each represented by only a single specimen) there are significant differences between sclerite means and variances (Tables 4 and 5). However, there is the less likely possibility that these differences may result from a series of founder effects.

Three isolating mechanisms can function to increase the efficiency of mating where related species coexist: habitat isolation, ethological isolation, and mechanical isolation (Bush 1975). The third problem with studies of character displacement is that usually only one of these mechanisms is explored by the study. Grant (1972) found that in some cases what passed for displacement involving morphological characters was actually the result of habitat isolation (Ripley 1959; Ficken et al. 1968). No comparative ecological data were available for *L. patagiata* and *L. sclopetaria*. However, they may occupy slightly different habitats, even though collected from the same locality.

Ethological isolation can also explain the separation of species. However, Robinson and Robinson's (1980) comprehensive study of courtship shows that although most congeneric orb-weavers share a series of courtship behaviors, there is much intraspecific variation. In such cases, differences in the external genitalia of males and females would enhance reproductive isolation, even if they were not the sole or even principal mechanism.

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POPULATION ECOLOGY OF *PARDOSA RAMULOSA* (ARANEAE, LYCOSIDAE) IN FLOODED RICE FIELDS OF NORTHERN CALIFORNIA

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ABSTRACT

The phenology, abundance, and habitat preferences of *Pardosa ramulosa* (McCook) in California rice fields were studied. Analysis of pitfall and floating sticky-trap samples showed that this spider apparently had one generation per year and overwintered in the immature stage. The population on the levees peaked in June and preceded the buildup in the paddies. Colonization of the paddies was possible after emergent vegetation was present. Before this *P. ramulosa* was observed being blown over the water surface. This may have contributed to its ability to disperse within the rice agroecosystem. In the paddies, *P. ramulosa* was associated with patches of aquatic broadleaf weeds where potential prey, including occasional pest species, was most abundant. *P. ramulosa* possesses many attributes thought to be desirable for a natural enemy in an annual agroecosystem, and may be an important predator of some pest species in rice.

INTRODUCTION

The importance of spiders as biological control agents has received considerable attention over the past two decades (see Luczak 1979; Riechert and Lockley 1984; Nyffeler and Benz 1987 for references). In spite of this, much controversy still remains concerning their perceived benefit. Clearly, much more information needs to be gathered (especially pertaining to the population and feeding ecology of spiders) before any definitive statement can be made regarding the role these generalist predators play in influencing prey levels. One habitat type where spiders appear to be a particularly important predator group is in swamp ecosystems, including flooded rice fields (Nyffeler and Benz 1987). We previously reported that *P. ramulosa* comprised ca 68% of all the spiders collected from California rice paddies, and suggested that it was the spider most likely to contribute to biological control in this agroecosystem (Oraze et al. 1988). Based on this and the importance of spiders found in rice fields in other parts of the world (Ito et al. 1962; Kiritani et al. 1972; Kiritani and Kakiya 1975; Kang and Kiritani 1978; Chiu 1979; Kenmore 1980), we felt additional study of *P. ramulosa* was warranted.

Various aspects of the population ecology of *P. ramulosa* have been studied in a number of habitats (Leigh and Hunter 1969; Yeargan and Cothran 1974; Van Dyke and Lowrie 1975; Hydorn 1977; Greenstone 1978), but little is known of its ecology in rice. The present study was undertaken to determine the phenology,

seasonal abundance and microhabitat preferences of *P. ramulosa* in California rice fields so as to better understand the potential of this predator for reducing insect pest levels.

MATERIALS AND METHODS

Phenology and seasonal abundance.—Ten pitfall and ten floating sticky traps were used to monitor *P. ramulosa* population fluctuations on the levees and in the paddies, respectively, at the Lattemore seedfield section of the Rice Experiment Station near Biggs, (Butte County) California. The traps were installed and serviced as described by Orazé et al. (1988). Both trap types were placed in designated locations for four to seven days once each month during the growing season. Additional sampling with pitfall traps was conducted throughout the fall and winter months between the 1984-85 growing seasons to determine overwintering phenology and abundance.

Habitat preference (paddy).—The abundances of *P. ramulosa* and potential prey items in vegetation types associated with the paddies were determined by randomized complete-block design experiments conducted at the Rice Experiment Station in 1984, and repeated with modifications in 1985. There were three treatments (vegetation types) in 1984 and two in 1985. Four blocks were used in both years. The experiments were located along the west margins of four adjacent fields in 1984 and along the east margins of two adjacent fields in 1985. Plots measured 6 by 6 m and were separated from one another by aluminum barriers that were 38 cm high and 6 m long.

The three treatments—rice only, rice plus weeds and weeds only—were achieved through various manipulations. In 1984 the rice was eliminated from the weedy plots by hand removal. This was followed with the transplanting of twenty-five duck salad (*Heteranthera limosa* (Sw.) Willd.) plants. In 1985 glyphosate at 1.12 kg (AI)/ha with a 1% solution of Herbimax® oil adjuvant was used to selectively remove the rice from the weedy plots. It was applied after the rice but before the weeds had emerged through the water. Transplanting of weeds was not necessary in 1985. In both years the species complex of the weedy plots consisted primarily of duck salad and monochoria (*Monochoria vaginalis* (Burm. f.) Presl.), with lesser amounts of California arrowhead (*Sagittaria montevidensis* Cham. and Schlecht.), waterplantain (*Alisma triviale* Pursh.), and roughseed bulrush (*Scirpus mucronatus* L.). The rice-only plots were treated with bentazon or 4EC MCPA at 1.12 kg (AI)/ha as required to remove the above-mentioned aquatic weeds. The rice plus weeds treatment of 1984 was left undisturbed.

The abundances of *P. ramulosa*, aster leafhopper (*Macrostelus fascifrons* Stål) and small flies (primarily Culicidae, Ephydriidae and Chironomidae) were obtained from floating sticky traps (one trap per plot) that were placed in the plots for a single seven-day sampling period. Aphid densities were estimated by taking five subsamples per plot with a UC-VAC suction device (Summers et al. 1984) and unit-area-sampler as described by Orazé et al. (1988). The mean number per sticky trap per day or the mean number per m² within each plot were transformed, $(X + 1/2)^{1/2}$, and analyzed with a two-way analysis of variance (1984) or paired *t*-test (1985).

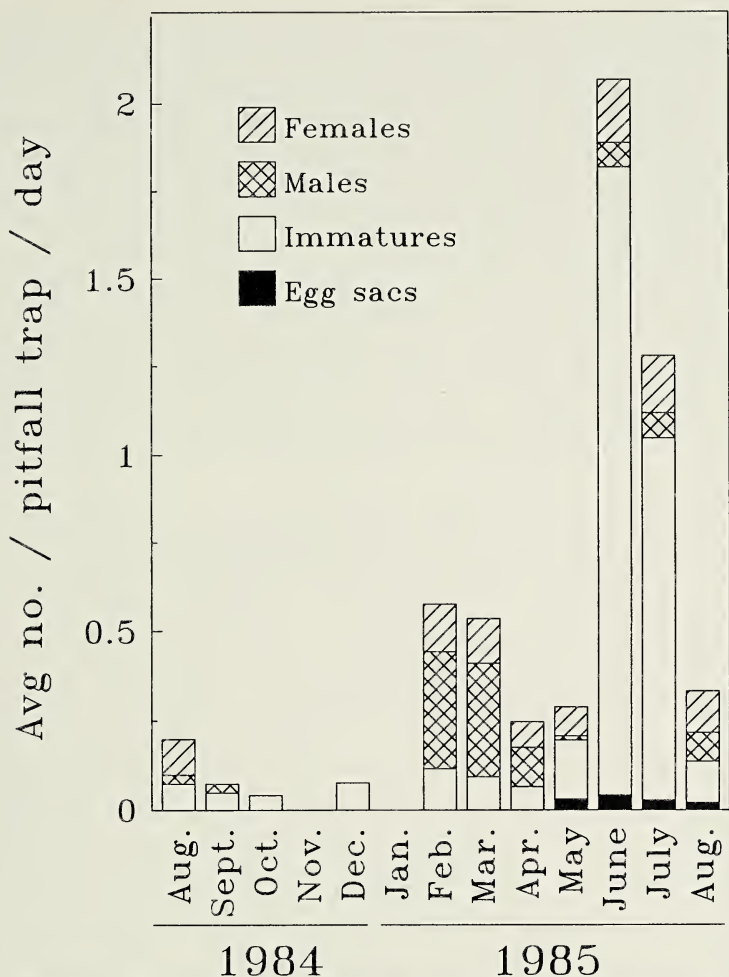


Figure 1.—Phenology and abundance of *Pardosa ramulosa* on rice field levees for 1984-85. Data obtained from a 4-7 day sampling period each month. Adults were separated from immatures by the presence of a fully developed palpal organ (males) or epigynum (females).

RESULTS AND DISCUSSION

Phenology and seasonal abundance.—It appears that *Pardosa ramulosa* had a single generation per year and overwintered in the immature stage, based on detailed analysis of pitfall-trap samples for 1984-85 (Fig. 1). These data, along with other data from trap catches, should be interpreted cautiously, as they reflect spider activity as well as abundance. Even so, similar conclusions have been reported for *P. ramulosa* in other habitats of northern California (Yeargan and Cothran 1974; Hydorn 1977).

The population peak on the levees occurred in June in each of the three years we sampled. In addition, the population decline on the levees coincided to some degree with the rise of the population in the paddies (Fig. 2A and B). This suggests that movement from the levees into the paddies contributed, at least in part, to the decline of the levee population. Similar seasonal movements have been described for *P. ramulosa* in other habitats (Hydorn 1977).

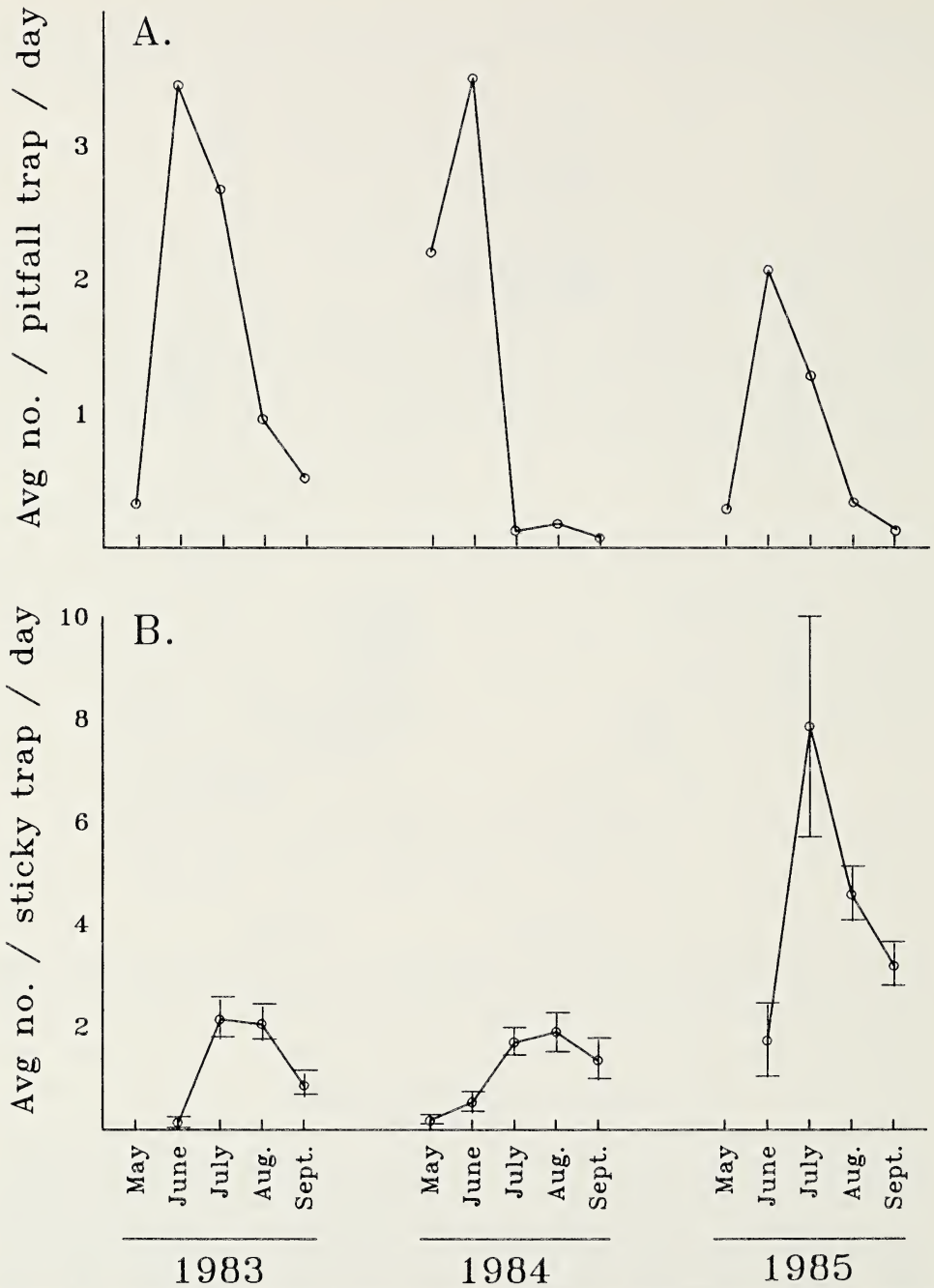


Figure 2.—Seasonal abundance of *Pardosa ramulosa* (adults and immatures) on levees (A), and in paddies (B) of flooded rice fields. Vertical lines represent SEM. No measure of variation could be calculated in "A" because of the combining of individual trap contents prior to counting.

The presumed dispersal from the levees into the paddies may be related to the seasonal succession of the paddy environment. Early in the cropping cycle, before emergent vegetation exists in the paddies, the spiders were apparently limited to the terrestrial habitats of the agroecosystem. If a spider was to walk into the

paddy at this time it would be blown across the water surface. This "sailing" was frequently observed as one of us (M.J.O.) walked along the paddy margins on a breezy day. A similar phenomenon was observed in a California salt marsh where *P. ramulosa* apparently "floated free" during intermittent tidal flooding. This appeared to have a pronounced influence on the daily movements of these spiders (Greenstone 1979a). "Sailing" may be the primary means by which *P. ramulosa* colonizes rice fields. Ballooning may also be a means of colonization, although the peak ballooning period of *P. ramulosa* does not coincide with the rice growing season (Yeargan 1975a). If *P. ramulosa* can successfully cross a flooded paddy by "sailing," then it would be possible for this species to quickly infiltrate large expanses of the agroecosystem. These spiders would probably initially accumulate on the margins and levees. Later, as plants emerge through the water, they could diffuse into or actively select the paddy habitat without being displaced by the wind, allowing the paddy population to become established and increase.

The abundance of *P. ramulosa* in the paddy typically declined late in the summer before the draining of the fields in September (Fig. 2B). Several factors may be responsible. Some that were observed, although not documented, included: cannibalism, possible interference and resource competition with another wolf spider, *Pirata piraticus* (Clerck) and predation from spider wasps (Pompilidae). Determination of the relative importance of these and other factors influencing the population dynamics of *P. ramulosa* in rice should be a challenging yet worthwhile endeavor.

A review of similar studies shows that *P. ramulosa* is abundant in a wide variety of habitats throughout California. These include annual agroecosystems such as rice (Oraze et al. 1988) and cotton (Leigh and Hunter 1969; Hickie 1981), perennial agroecosystems such as alfalfa (Yeargan and Dondale 1974; Hickie 1981), relatively undisturbed areas with "wild" vegetation such as salt marshes (Garcia and Schlinger 1972; Greenstone 1978) and sewage oxidation ponds (Hydorn 1977), and finally backyard lawns (Van Dyke and Lowrie 1975). The ability of *P. ramulosa* to inhabit such a diverse array of habitats (from coastal salt marshes to irrigated desert cotton fields) indicates that it probably possesses broad physiological tolerances and flexible behavior patterns. One might expect to find this spider wherever its moisture requirements are satisfied within its range. This may include more habitats than would be initially obvious. For example, soil cracks appeared to provide *P. ramulosa* refuge between irrigations in alfalfa and cotton fields (Yeargan and Cothran 1974; Hickie 1981) and in some ephemeral aquatic habitats such as vernal ponds (Hydorn 1977; Greenstone 1980).

Habitat preference (paddy).—Plant type in the paddy had a significant influence on *P. ramulosa* abundance. *P. ramulosa* and nearly all of the potential prey types sampled were significantly more abundant in the weedy plots in both the 1984 and 1985 experiments (Tables 1 and 2). The weeds in the rice plus weeds treatment of the 1984 experiment eventually perished. This resulted in plots that were essentially the same as the rice-only plots by the time the samples were taken. There were no significant differences in the arthropod species sampled between these two treatments. Because of this, the rice plus weeds treatment was not included in the 1985 experiment.

Pardosa ramulosa associated in microhabitats of the paddy where potential prey, some of which are occasional pests of rice (e.g., aster leafhopper,

Table 1.—Mean number \pm SEM of *Pardosa ramulosa* and potential prey in vegetation types associated with rice field paddies. Biggs, Calif. 1984. Samples were taken on 27 July 1984. Column means followed by the same letter are not significantly different ($P < 0.01$, Tukey's HSD method) (Systat Inc. 1987). Transformed data, $(X + 1/2)^{1/2}$, were analyzed with a two-way ANOVA, $df = 2,3$.

Vegetation type	Avg. no. per sticky trap per day			Avg. no. per m ²
	<i>Paradosa ramulosa</i>	Aster leafhopper	Small flies	Aphids
Rice	0.6 \pm 0.1 a	0.4 \pm 0.3 a	4.5 \pm 1.5 a	208.3 \pm 125.8 a
Rice + weeds	0.3 \pm 0.1 a	0.2 \pm 0.1 a	4.8 \pm 1.2 a	225.5 \pm 110.4 a
Weeds	2.8 \pm 0.3 b	11.3 \pm 1.6 b	41.5 \pm 4.1 b	5795.3 \pm 3423.2 b
<i>F</i> statistic	73.221	55.148	82.933	8.825
<i>P</i> value	<0.000	<0.000	<0.000	0.018

mosquitoes, seed midges and leaf miners), were most abundant. This behavior does not appear to be unusual for spiders (Riechert and Lockley 1984). However, in a related study Greenstone (1978) found no correlation between prey availability and *P. ramulosa* density among the small pools from which he sampled in an estuarine salt marsh. He noted that the spiders reached their highest densities along the margins of the pools, irrespective of prey availability, even though this varied enormously among pools. If *P. ramulosa* actively selected weedy areas of the rice paddy, as the data of this study suggest, then it is not clear exactly to what factor(s) (e.g., prey availability, temperature-humidity regime, cover for protection, etc.) *P. ramulosa* was responding. This would seem to be a fruitful area for future research.

Pardosa ramulosa exhibited characteristics that are thought to be desirable for a natural enemy in an annual agroecosystem (Ehler and Miller 1978). It was a good colonizer, probably because of its "sailing" ability. It appears to have broad physiological tolerances and the behavioral flexibility (based on its occurrence in a number of very diverse ecosystems, as was discussed earlier) that probably help it to survive the adverse conditions that typically exist during the early phases of a cropping cycle. In addition, perceived limitations of generalist predators (like *P. ramulosa*) such as cannibalism, territoriality (Hydorn 1977) and polyphagy (Yeargan 1975b; Greenstone 1979b) might also enhance early season survivability by mitigating the effects of temporal shortages of preferred prey. Finally, *P. ramulosa* preceded potential pests into the paddy and later associated in microhabitats where they were most abundant. Based on these findings, the role of *P. ramulosa* in reducing levels of selected pests in California rice should be investigated.

Table 2.—Mean number \pm SEM of *Pardosa ramulosa* and potential prey in vegetation types associated with rice field paddies. Biggs, Calif. 1985. Samples were taken on 30 July 1985. Column means followed by the same letter are not significantly different ($P < 0.05$). Transformed data, $(X + 1/2)^{1/2}$, were analyzed with a paired *t*-test, $df = 1,3$.

Vegetation type	Avg. no. per sticky trap per day			Avg. no. per m ²
	<i>Paradosa ramulosa</i>	Aster leafhopper	Small flies	Aphids
Rice	1.0 \pm 0.1 a	14.0 \pm 3.3 a	21.7 \pm 8.4 a	22.2 \pm 6.2 a
Weeds	2.9 \pm 0.6 b	38.9 \pm 10.0 b	51.5 \pm 13.2 a	474.3 \pm 169.8 b
<i>t</i> statistic	23.392	11.603	4.108	14.284
<i>P</i> value	0.017	0.042	0.136	0.032

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DIET-INDUCED COLOR CHANGE IN THE HAWAIIAN HAPPY-FACE SPIDER *THERIDION GRALLATOR*, (ARANEAE, THERIDIIDAE)

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ABSTRACT

The Hawaiian happy-face spider *Theridion grallator* Simon is a small spider, endemic to Hawaii, where it is found under leaves in the wet and mesic forests. The abdomen is pale, translucent yellow, but variable amounts of red, black or white pigment may be superimposed on this to generate a host of patterned morphs. The translucence of the abdomen may enhance crypsis against predators searching the underside of leaves; the variability in the superimposed pattern may serve to counteract the development of a search image by the predator. The present study documents plasticity in base coloration, which can change rapidly and markedly following ingestion of certain types of prey. This may be merely a consequence of abdominal translucence. But it is interesting to note that it adds a whole new dimension to the color polymorphism of the species.

INTRODUCTION

Color change in animals is a widespread phenomenon. It is generally associated with a change in physiological state. This in turn may be induced by ontogenetic or environmental changes, or stress. In spiders, color change is known to occur under a variety of circumstances. Ontogenetic modifications are widespread, with the adult coloration being attained in the final molt (Bonnet 1933; Homann 1946; Millot 1949). More rapid changes in color pattern have been noted in spiders of the family Araneidae, which accumulate guanine beneath the cuticle during periods of starvation, thereby developing a pattern of opaque white blotches over the abdomen (Foelix 1979).

Reversible color change has been most extensively documented in the crab spider *Misumena vatia* (Clerck) (Packard 1905; Gadeau de Kerville 1907; Rabaud 1923; Gabritschewsky 1927; Weigel 1941; Hinton 1976). This spider is usually whitish and sits on white flowers. If it moves to a flower of another color it can, by transferring a liquid pigmented material to the cuticle, change to the color of its new substrate. However, the transformation takes about 10 days to occur, and it is limited to pastel yellows and pinks. Similar reversible color changes have been found to occur in other crab spiders (Heckel 1891; Bristowe 1958) as well as the lynx spider *Peucetia viridans* (Hentz) (Oxyopidae) (Neck 1978).

The most rapid reversible changes to date are found in various Araneid spiders, as a result of migration of chromatic inclusions or retraction of guanocytes

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(Blanke 1975). The Australian *Phonognatha wagneri* Simon, for example, drops from its web when disturbed, the abdomen simultaneously changing from cream to brown (Roberts 1936). A similar phenomenon has been documented in *Leucauge subgemma* Bos. et Str. and *Chrysso venusta* (Yaginuma) (Uyemura 1957), *Floronina bucculenta* (Clerck) (Bristowe 1958), *Gea heptagon* (Hentz) (Sabath 1969) and *Cyrtophora cicatrosa* (Stoliczka) (Blanke 1975).

Rapid color change following dietary ingestion has not been documented in spiders. In this paper I demonstrate the phenomenon in the Hawaiian happy-face spider *Theridion grallator* (Simon). *T. grallator* is a small (up to 4.5 mm) spider endemic to the Hawaiian Islands, where it inhabits the underside of leaves of a variety of plants, especially the native *Broussaisia arguta* (Saxifragaceae) and *Clermontia arborescens* (Campanulaceae). The spider has a base color of pale, translucent yellow, but may exhibit a variety of abdominal color patterns (red, black or white) superimposed on this base color. The predominant color morph has no pattern (or a series of small black dots only); patterned morphs, although generally less common, are diverse in form and extent of pigment.

The study was initiated following a chance observation: while monitoring marked spiders (paint marks on certain legs), I observed an individual change base coloration from translucent yellow to bright orange. Here I examine the nature of diet-induced changes in base color, and possible functions of the phenomenon. To what extent can spiders change the base color of the abdomen, and do prey items that are normally included in their diet induce reversible color change? The polymorphic nature of the pattern superimposed on the base color is considered elsewhere (Gillespie and Tabashnik in press).

METHODS

The rate and extent to which *T. grallator* is capable of changing its color was determined by keeping individuals in vials and allowing them to drink from cotton swabs saturated with food coloring (red, green, blue and black). Spiders in control vials had cotton swabs saturated with water only.

Individuals of *T. grallator* were then given a variety of insects that they might capture in their natural environment. These were primarily Diptera: Drosophilidae in the size range 2-4 mm ($N = 11$) and 5-6 mm ($N = 5$) and Dolichopodidae in the size range 2-4 mm ($N = 9$). Lepidoptera (one adult moth and two larvae), Homoptera (Cicadellidae, $N = 3$) and Araneae (Theridiidae, $N = 1$) were also used to determine their effect on the base color of *T. grallator*.

Field observations were made on populations of *T. grallator* in native forest (mixed Ohi'a—Koa) in the Nature Conservancy of Hawaii's Waikamoi Preserve on Maui, near the common boundary of the Preserve and the Makawao State Forest at 1360 m elevation. Spiders were located by thorough scrutiny of leaves of *Broussaisia arguta* and *Clermontia arborescens* in an area of approximately 1 hectare, and were marked with small dots of paint on a leg. Individuals were monitored once every two days between October 1987 and April 1988. Whenever a spider was found to be feeding on prey, it was watched for any subsequent color change. The duration of the color change (the period from the initial observation of feeding until it reverted to the original translucent yellow) was determined by checking color on subsequent days. Color changes in marked

Table 1.—Change in color from pale yellow as a consequence of prey ingestion by the Hawaiian happy-face spider *Theridion grallator*. Spiders were fed prey collected from the Waikamoi study site. The color change induced in the opisthosoma of the spider by a particular prey item, and the duration of the color change before the spider reverted to pale yellow, were all recorded. *N* = number of spiders observed.

Prey	<i>N</i>	Color change	Duration (days)
DIPTERA			
<i>Drosophila</i> , 2-4 mm	11	Orange	2
<i>Drosophila</i> , 5-6 mm	5	Orange	3
Dolichopodidae, 2-4 mm	9	Orange	2
LEPIDOPTERA			
Adult moth	1	Dark orange	
Caterpillar	2	Green	4-6
HOMOPTERA			
Cicadellidae, 2-4 mm	3	Green	2-3
ARANEAE			
Theridiidae, 2-4 mm	1	Orange	2

spiders were also monitored when feeding was not directly observed. This allowed an estimate of the range of base colors the spiders could exhibit under natural conditions, and their relative frequency.

In order to determine the generality of the phenomenon of color change following dietary ingestion, species from two other genera of the Theridiidae and one from the closely related Nesticidae, were tested for color changes induced by intake of food coloring. The species were chosen on the basis of degree of pigmentation of the abdomen, and were all from southeastern Tennessee. *Nesticus barri* Gertsch is a pale, translucent yellow, essentially eyeless troglobite; it was collected from Lost Cove Cave, near Sewanee, Tennessee. *Achaeearanea tepidariorum* (C. L. Koch), an extremely common spider found throughout the United States, has a dirty white abdomen with gray markings. *Latrodectus mactans* (Fabricius) has a shiny black abdomen, with a red "hourglass" mark on the venter. Both *A. tepidariorum* and *L. mactans* were collected in Sewanee, Tennessee. Individuals of each of these species (five *N. barri*, five *A. tepidariorum* and two *L. mactans*) were placed in vials with swabs of red and green food coloring (and water as control). Spiders were observed as they ingested the food coloring, and monitored for changes in color over the next 7 days. Individuals were then exposed to the second food color.

RESULTS

When placed in a vial, *T. grallator* readily ingested food coloring from the cotton swabs. The color could be seen running into the abdominal section of the intestine within 5-10 s, and infusing it with color within 1 min. The dye then accumulated in the Malpighian tubules before being excreted after an average of 3.5 (SD = 1.6) days.

A similar effect was found when *T. grallator* was fed prey collected from the Waikamoi study site. Table 1 summarizes the color changes that were observed. The color generally changed from translucent yellow to either orange (following ingestion of various Diptera or adult Lepidoptera) or green (after ingestion of larval Lepidoptera and adult Homoptera). The abdomen retained the color for 2-

Table 2.—Overall frequency of color changes in natural populations of *T. grallator*: marked individuals that were found to have changed color, whether or not the prey capture event itself was observed ($N = 82$). Where prey capture was observed ($N = 11$), the approximate duration of each color change (to the nearest day) was determined. The prey inducing the change of color to chocolate was observed on neither occasion; but both these spiders retained their color for 7 days after the change was initially observed.

Color	Proportion	Average duration (days)
Orange	81%	2-4
Green	17%	4-6
Chocolate	2%	>7

6 days, retention time probably being a function of the amount of pigment ingested.

The frequency of color changes in natural populations of *T. grallator* (marked individuals that were found to have changed color, whether or not the prey capture event itself was observed) are shown in Table 2. As can be seen, the most common color change was that from translucent yellow to orange, reflecting the fact that small dipterans comprise approximately 70% of the dietary intake of *T. grallator* (Gon 1985). On two occasions, the base color was found to have changed to very dark chocolate brown. It is not known what prey item these individuals had consumed.

The three other species tested for susceptibility to color change following ingestion of food coloring varied widely in their response. *N. barri* changed color in a manner similar to *T. grallator*. The red and green food coloring suffused the abdomen within 1 minute; the dye was excreted after 2-3 days (average 2.7 days). *A. tepidariorum* showed a definite, but very much weaker, response. The colors became interspersed between the white dots of guanine, giving a mottled appearance to the abdomen. In *L. mactans*, the food coloring could be seen as a slight red or green tinge to the black abdomen. The color did not suffuse the abdomen, but rather appeared as a folium, the pattern probably dictated by the digestive diverticula.

DISCUSSION

The Hawaiian happy-face spider is capable of passively changing base coloration according to dietary intake. Such rapid and reversible color changes following ingestion have never before been documented in spiders. But, as I have shown here, other species of spiders can also change color when they ingest dyes. The degree to which spiders are capable of diet-induced color change appears to be a function of their translucence. The heavily pigmented *L. mactans* showed a barely discernible color change. In *A. tepidariorum*, the ingested dye was seen as spots interspersed between the natural pigment and guanine crystals on the abdomen. Under natural conditions, pigments from prey will tend to be ingested in much smaller amounts, and their effects on abdominal coloration considerably more subtle. In *N. barri*, however, the ingested dye suffused the entire abdomen in a manner similar to that observed for *T. grallator*. *N. barri* may also demonstrate observable color change under natural conditions if it ingests pigmented prey. Indeed, although prey capture was not observed, two individuals

of this species have been found in the cave with black (as opposed to the usual pale, translucent yellow) abdomens.

What are the selective forces responsible for degree of pigmentation in spiders? Nearly all spiders—in common with insects—have some kind of integumental pigment, which may serve to protect them from radiation (ultraviolet), to regulate temperature, and may also function in protection from predation (Holl 1987). Complete depigmentation is a characteristic of obligate cavernicoles (Gertsch 1984). Yet *T. grallator*, an inhabitant of the Hawaiian forests, has a translucent base color similar to the troglobitic *N. barri*. What evolutionary forces might be implicated in the loss of pigment in this terrestrial species?

One of the most abundant groups of insectivores in Hawaiian forests are the honeycreepers (Perkins 1913). In Maui's Waikamoi Preserve, the most common insect gleaner is the Maui Creeper, *Parareomyza montana*, whose behavior of searching the underside of leaves resembles that of the creeper family Certhidae (Scott et al. 1986). *T. grallator* occupies the underside of leaves. To the human eye, the translucence of these spiders renders them almost invisible against the light filtering through the leaf when viewed from below. Birds may encounter the same difficulty when searching for prey. Avoidance of predation may well have played a major role in the depigmentation of *T. grallator*.

Diet-induced color change in *T. grallator* may merely be an inevitable consequence of its translucence. Yet it is interesting to note that this spider is highly polymorphic. Although the base color of the abdomen is translucent yellow and many individuals exhibit this base color alone, others exhibit a host of superimposed patterns of red, black and white patches. These patterns are under genetic control and are inherited as a simple Mendelian trait (Gillespie and Tabashnik in press). Diet-induced color change adds an entirely new dimension to the enormous array of color morphs that the species can exhibit. Could there be any advantage to an individual in widening its spectrum of color morphs?

If there is any selective force operational here, it is most likely to be the avoidance of predation by birds. A common tendency in birds is the development of a search image (Clarke 1962; Allen 1974, 1976; Murdoch and Oaten 1975; Atkinson and Warwick 1983; Greenwood 1984; but see Guilford and Dawkins 1987). Studies have implicated the development of such search images in the generation of interindividual variability in color patterns of the prey involved (Endler 1978; Rettenmeyer 1970). Selection under these conditions will tend to favor the less common morphs, which will consequently increase until numbers are sufficient to allow the avian predators to develop a search image towards them. It is possible that strong selection for abnormal color patterns is the primary selective force generating variability in coloration of *T. grallator*, whether this is genetically determined or environmentally plastic—a passive consequence of dietary ingestion.

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SEX-BIASED PREDATION BY WEB-SPINNING SPIDERS (ARANEAE) ON SPRUCE BUDWORM MOTHS

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ABSTRACT

Web-spinning spiders of 6 families, 12 genera, and at least 15 species preyed on spruce budworm, *Choristoneura fumiferana* (Clem.), moths in Maine. Significantly more (G -tests, $P \leq 0.05$) male than female moths were captured by 9 web-spinner species, and the overall capture by spiders was significantly biased ($P \leq 0.001$) toward male moths. Most of the budworm-moth prey were found in webs of *Frontinella pyramitela* (Walck.) (30.6%) and *Theridion pictum* (Walck.) (45.0%). Multiple observations of the same web (temporal replication) indicated that *T. pictum* captured significantly more ($Z = -4.36$, $P = 0.000$) budworm moths/web than *F. pyramitela*. However, such differences in prey-capture rates were not detected ($Z = -1.49$, $P = 0.14$) over several locations (spatial replication). Web surveys during the spruce budworm's moth-flight period indicated that percentages of webs with budworm prey were about equal; *F. pyramitela* ($\bar{X} = 19.5 \pm 5.7$), *T. pictum* ($\bar{X} = 18.9 \pm 3.6$), all species ($\bar{X} = 16.0 \pm 2.7$).

Trees occupied by *T. pictum* were significantly taller ($P \leq 0.001$) and webs significantly higher ($P \leq 0.001$) than trees and webs of *F. pyramitela*. For both spider species, mean relative web height was $> 60\%$ of tree height, possibly indicating nonrandom choices of foraging patch. However, tree height and web height were not significantly ($P \geq 0.05$) related to prey-capture for *F. pyramitela* webs; tree height was significantly taller ($P = 0.009$) for *T. pictum* webs with budworm moths. Two species of kleptoparasites, *Argyrodes trigonum* (Hentz) and *A. fictilium* (Hentz), were associated with host-spider webs that captured spruce budworm moths.

Possible explanations for the observed sex-biased predation include: 1) sex-pheromone mimicry, 2) uneven prey densities, 3) accidental capture, 4) moth behavior, and 5) moth-flight activity. Because of the potential impacts on spruce budworm reproduction, predation by spiders gains increased importance as a source of moth mortality.

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INTRODUCTION

The spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae), is the most destructive defoliator of coniferous forests in the northeastern United States and Canada (Kucera and Orr 1981). Recent devastating outbreaks of this forest pest have renewed interest in determining the natural enemies—pathogens, parasites, and predators—that cause mortality to the spruce budworm. Spiders have long been recognized as predators of the spruce budworm (Johannsen 1913; Tothill 1923). Although all life stages of the spruce budworm—eggs, larvae, pupae, and moths—are susceptible to predation by spiders (Jennings and Crawford 1985), most observations concern spiders feeding on budworm larvae (Jaynes and Speers 1949; Loughton et al. 1963; Renault and Miller 1972). Few investigators have focused attention on spiders that prey on spruce budworm moths; Jennings and Crawford (1985) listed 10 species of web-spinning spiders that captured moths of *C. fumiferana* in their webs in Maine. Turnbull (1956) observed predation by both web-spinning and vagrant spiders on budworm moths in British Columbia; however, his observations pertain to the western spruce budworm, *C. occidentalis* Freeman.

In this paper we describe predation by several species of web-spinning spiders on moths of *C. fumiferana* in Maine, compare differential mortality between moth sexes, and discuss possible factors that contribute to sex-biased predation on male moths.

METHODS

Study sites.—All observations were made in spruce-fir (*Picea-Abies*) forests that were infested with the spruce budworm. Individual study sites were distributed in a band from northwestern to southeastern Maine (Fig. 1). Study-site abbreviations, locations (by organized town or township), and observation years were:

(SOL)—Soldiertown Twp., T2 R3, Somerset County, 1979.

(WES)—West Middlesex, Canal Grant, Somerset County, 1979.

(TOM)—Tomhegan Twp., Somerset County, 1979.

(KOK)—Kokajo, T1 R13 WELS, Piscataquis County, 1977.

(GRE)—NE of Greenville, T2 R12 WELS, Piscataquis County, 1978.

(SHA)—Shawtown Twp., Piscataquis County, 1979.

(TEL)—Telos, T5 R11 WELS, Piscataquis County, 1978.

(COF)—Coffeelos, T6 R11 WELS, Piscataquis County, 1978.

(MIL)—Milo, Piscataquis County, 1979.

(MED)—Medford, Piscataquis County, 1978, 79, 80, 81.

(HOW)—Howland, Penobscot County, 1978, 79, 80.

(PAS)—Passadumkeag, Penobscot County, 1979.

(PEF)—Penobscot Expt'l Forest, Bradley, Penobscot County, 1978, 79, 80, 81, 82.

(MAT)—Mattakeunk, Lee, Penobscot County, 1979.

(STE)—West of Steuben, T7 SD, Hancock County, 1985.

(T19)—T19 ED BPP, Washington County, 1979.

(T18)—T18 ED BPP, Washington County, 1979.

(P14)—No. 14 Plantation, Washington County, 1979, 81.

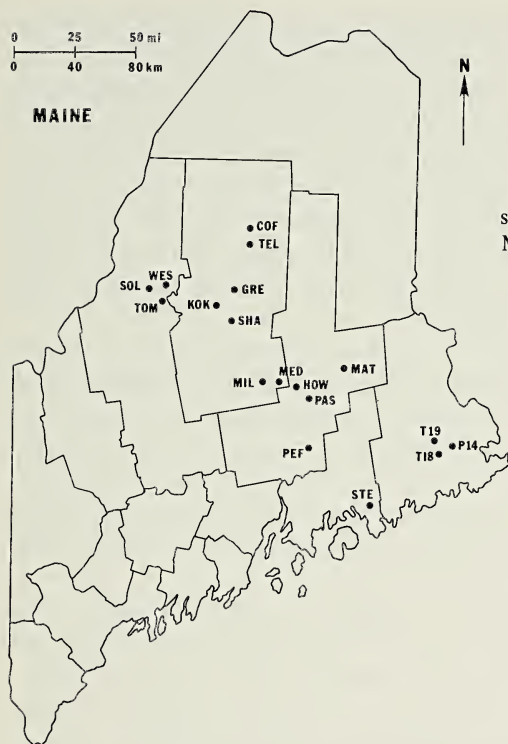


Figure 1.—Study-site locations for web-spinning spiders that prey on spruce budworm moths in Maine (see text for list of site abbreviations).

Most study sites were in cutover spruce-fir stands with abundant natural regeneration of balsam fir, *Abies balsamea* (L.) Mill., and red spruce, *Picea rubens* Sarg., or white spruce, *P. glauca* (Moench) Voss, in the understory. Observations were confined to accessible webs in small trees (most ≤ 3 m in height) and in lower crowns of intermediate-height trees (≤ 5.5 m). All trees were in the understory and grew in forest openings, e.g., along old logging roads and trails. Forest-stand measurements were not taken; however, balsam fir was the prominent understory species.

Study periods.—We observed spider predation on spruce budworm moths during the peak years (1977-82) of a budworm epidemic in Maine. A few observations were made during the decline phase of the same epidemic in 1985. Each study year, webs of web-spinning spiders were examined for moth prey during the spruce budworm's moth-flight period. In Maine, budworm moth flight begins in late June, peaks in early to mid-July, and ceases by late July or early August (Houseweart et al. 1982; Kendall et al. 1982; Jennings et al. 1984). Male moths of the spruce budworm generally emerge from pupae 1 or 2 days earlier than female moths, and most moths live for about 10 days (Greenbank et al. 1980). Because of seasonal variation in development, moth activity at a site lasts about 3 weeks, but can be extended longer by invasion of dispersing moths (Greenbank et al. 1980). We made detailed observations every 2-10 days at three sites, Greenville (GRE), Medford (MED), and Penobscot Experimental Forest (PEF); observations at remaining sites were intermittent but within the budworm's moth-flight period.

Predator-prey collections.—At all study sites, we examined spider webs on understory coniferous trees *ad libitum* (i.e., as encountered) and collected both

spider(s) and any ensnared moth prey. Most of the spiders we studied in Maine either left cadavers of spruce budworm moths in their webs (*Frontinella*) or incorporated the cadavers into web retreats (*Theridion*). Occasionally, prey cadavers were found wrapped in silk and dropped below the web (*Theridion*), or hung in prey middens (*Cyclosa*), or hung in web supports (*Neoscona*). Some unwrapped prey were found discarded immediately below the web (*Prolinyphia*). To minimize disturbance, the resident spider was captured first and then prey removed from the web or substrate with forceps. Field-collected spiders and their prey were placed in 2-dram vials containing 70% ethanol, labeled, and transported to the laboratory for identification.

Not all available webs were examined at each site, nor were all observed spiders with budworm prey collected. However, when a spider-prey collection was made, we removed *all* spruce budworm moths from the web or immediately below the web. Our goal was to collect a representative sample of web-spinning spiders that captured spruce budworm moths in the readily accessible understory.

Web surveys.—In addition to predator-prey collections, we inventoried spider webs and their ensnared prey at various locations. Two survey methods were used to provide temporal and spatial replication.

1) *Temporal replication*: At Greenville (GRE), Medford (MED), and Penobscot Experimental Forest (PEF), webs of the two most commonly encountered species—*Frontinella pyramitela* (Walck.) and *Theridion pictum* (Walck.)—were identified and tagged on 20-22 small trees/site. Numbers of webs by species and site were: *F. pyramitela*—MED ($n = 20$), PEF ($n = 53$); *T. pictum*—GRE ($n = 55$), MED ($n = 10$). Both species spin their webs in young understory spruce or fir trees; each species builds a characteristic web. The sheetline weaver *F. pyramitela* spins a “bowl and doily” web consisting of a shallow bowl, a horizontal sheet beneath the bowl, and a meshwork of silk that forms a barrier above the bowl (Comstock 1948). The theridiid *T. pictum* constructs a tangle web of many viscid threads, above which the spider ties several spruce or fir needles together to form a dome-shaped tent in which to hide (Emerton 1927). Cadavers of spruce budworm moths and other prey often are incorporated into the silken walls of the tent; occasionally, prey is hung in the tangle web or dropped to branches below the web.

Tagged trees and webs were revisited at intervals of 2-10 days ($\bar{X} = 5.5$ days) and data recorded on spider-web occupancy and prey captures. In most instances we gently removed all ensnared moths from the tagged webs for prey identification and prey-sex determination. There was minimal web disturbance. Occasionally however, budworm moths were field-identified (but not sexed), counted, and left intact in the webs. Tagged-web observations spanned the initial period (late June, $n = 2$ visits/site) and peak (mid-July, $n = 3-4$ visits/site) in spruce budworm moth-flight activity.

2) *Spatial replication*: At each of the aforementioned sites plus Howland (HOW), Coffeelos (COF), and Telos (TEL), 30 webs (any species) were examined *ad libitum* and numbers of budworm prey/web recorded. Field identifications were made of *F. pyramitela* and *T. pictum*; specimens of unrecognized species were collected for later identification. Cadavers of spruce budworm moths were removed from webs for prey-sex determination. All 30-web inventories (1-3/site) were made during the spruce budworm's moth-flight period in late June ($n = 2$) and July ($n = 7$).

Tree-web heights.—At some study sites, measurements were taken of tree and web height (m) above ground for *F. pyramitela* and *T. pictum*. Tree height was measured from ground to uppermost terminal-shoot level; web height was measured from ground to bowl level (*Frontinella*) and tent level (*Theridion*).

Spider identifications.—Collected spiders were identified by the senior author; species determinations follow Kaston (1981) and other consulted sources including revisions by Chamberlin and Gertsch (1958), Berman and Levi (1971), and Levi (1957, 1974). Only sexually mature spiders were identified to species; juveniles, including penultimate males, were identified to generic level. Representative specimens of all identified species are deposited in the arachnid collection, U.S. National Museum of Natural History, Washington, DC.

Prey-sex determinations.—All moth cadavers removed from spider webs were examined microscopically and their genitalia compared with published descriptions of the male (Outram 1970) and female (Outram 1971) reproductive systems of the spruce budworm. Such examinations allowed confirmation of field-identified prey species and determination of prey sex. A few collected moths (< 5%) were devoid of genitalia, i.e., the posterior abdominal segments were missing—possibly lost during collection, discarded by the spider, or removed by scavengers. Remains of these damaged moths were identified by their general morphology (Freeman 1947) and compared with known, identified specimens; they were sexed by tibial-spur length (long, male; short, female) and shape of the scutellum.

Data analyses.—Because the spruce budworm has a sex ratio that does not vary markedly from 1:1 (Miller 1963), we hypothesized an equal representation of the sexes (male, female) among budworm moth-prey captured by web-spinning spiders. We used the *G*-statistic for log-likelihood ratios (Sokal and Rohlf 1981) to test observed vs. expected frequencies of moth sexes among prey captures for individual and over all spider species. The null hypothesis for expected frequency was 50% male, 50% female moths. Resultant *G*-values were compared with the chi-square distribution at $P = 0.05$.

Means, standard errors, and coefficients of variation were calculated for tree- and web-height measurements for *F. pyramitela* and *T. pictum*. We also calculated relative web height (Toft 1987) for both species by the formula: rel. web ht. = web ht./tree ht. \times 100. The Wilcoxon's two-sample test (Sokal and Rohlf 1981) was used for comparisons of means (tree ht., web ht., rel. web ht.) between spider species at $P = 0.05$. Spearman's rank correlation coefficient (ρ) was used to determine the degree of association between tree- and web-height variates for each species.

RESULTS

Spider taxa.—Web-spinning spiders of 6 families, 12 genera, and at least 15 species were observed with spruce budworm moth prey in Maine (Table 1). Almost all of the budworm prey captures were made by female spiders; a single male of *Agelenopsis utahana* (Chamberlin & Ivie) was collected with budworm-moth prey; a few webs of *F. pyramitela* (1), *Prolinyphia marginata* (C. L. Koch) (2) and *Theridion murarium* Emerton (1) were cohabited by both spider sexes and contained cadavers of spruce budworm moths. At Medford (MED), we

Table 1.—Species of web-spinning spiders observed for spruce budworm moth prey, 18 localities, spruce-fir forests of Maine; all study years combined. The *G*-statistic for log-likelihood ratios (Sokal and Rohlf 1981) was used to compare observed vs. expected frequencies of moth sexes among prey captures (loc = localities, obs = observed, SBW = spruce budworm, ns = not significant, $P > 0.05$, * = includes multiple observations of some webs).

FAMILY	<i>n</i> loc	<i>n</i> webs obs	<i>n</i> webs with SBW prey	Σ SWB prey		<i>G</i>	<i>P</i>
Species				Males	Females		
AGELENIDAE							
<i>Agelenopsis utahana</i> (Chamb. & Ivie)	1	1	1	1	0	1.39	ns
<i>Agelenopsis</i> sp.	2	2	2	3	0	4.16	≤0.05
ARANEIDAE							
<i>Araneus nordmanni</i> (Thorell)	1	1	0				
<i>Araneus marmoreus</i> Clerck	1	1	0				
<i>Araneus</i> sp.	4	5	3	3	0	4.16	≤0.05
<i>Araniella displicata</i> (Hentz)	5	6	4	4	0	5.54	≤0.05
<i>Cyclosa conica</i> (Pallas)	5	10	3	3	0	4.16	≤0.05
<i>Cyclosa</i> sp.	1	3	0				
<i>Neoscona arabesca</i> (Walck.)	3	10	1	0	1	1.39	ns
<i>Neoscona</i> sp.	7	31	28	35	2	35.73	≤0.001
<i>Nuctenea patagiata</i> (Clerck)	1	1	1	1	0	1.39	ns
<i>Nuctenea</i> sp.	1	1	1	1	0	1.39	ns
DICTYNIDAE							
<i>Dictyna phylax</i> Gertsch & Ivie	1	1	1	1	0	1.39	ns
<i>Dictyna</i> sp.	1	1	1	1	0	1.39	ns
LINYPHIIDAE							
<i>Frontinella pyramitela</i> (Walck.)	14	420*	98	129	9	124.77	≤0.001
<i>Pityohyphantes costatus</i> (Hentz)	7	11	8	9	0	12.48	≤0.001
<i>Pityohyphantes</i> sp.	5	7	0				
<i>Prolinyphia marginata</i> (C.L. Koch).	7	31	18	18	2	14.72	≤0.001
<i>Prolinyphia</i> sp.	1	1	0				
TETRAGNATHIIDAE							
<i>Tetragnatha versicolor</i> Walck.	4	6	2	2	0	2.77	ns
THERIDIIDAE							
<i>Theridion differens</i> Emerton	4	26	4	5	1	2.91	ns
<i>Theridion frondeum</i> Hentz	4	5	3	3	1	1.05	ns
<i>Theridion murarium</i> Emerton	12	17	10	8	5	0.70	ns
<i>Theridion pictum</i> (Walck.)	11	564*	172	175	28	118.53	≤0.001
<i>Theridion</i> spp.	2	8	0				
All species	18	1170*	361	402	49	315.22	≤0.001

observed a male and female of *P. marginata* sharing prey, i.e., both spiders were feeding on the same male budworm moth. Juveniles of *Agelenopsis*, *Araneus*, *Dictyna*, *Neoscona*, and *Nuctenea* were observed with budworm moth prey, whereas juveniles of *Cyclosa*, *Pityohyphantes*, *Prolinyphia*, and *Theridion* were not.

Moth-prey numbers.—Numbers of budworm moths/web ranged from 1-5 for *F. pyramitela*, and from 1-14 for *T. pictum*; numbers for the remaining species

seldom exceeded 2 moths/web. For multiple observations of the same web (temporal replication), mean budworm moths/web was significantly higher ($Z = -4.36$, $P = 0.000$) for *T. pictum* ($\bar{X} = 0.41 \pm 0.07$, $n = 301$) than for *F. pyramitela* ($\bar{X} = 0.07 \pm 0.02$, $n = 168$). However, such differences in prey-capture rates between spider species were not detected ($Z = -1.49$, $P = 0.14$) when several localities (spatial replication) were considered; *F. pyramitela* ($\bar{X} = 0.52 \pm 0.05$, $n = 252$) and *T. pictum* ($\bar{X} = 0.63 \pm 0.06$, $n = 263$).

Moth-prey sex.—A total of 402 male and 49 female moths of the spruce budworm were collected from spider webs (all species) in Maine (Table 1). Most of the budworm moths were retrieved from webs of *F. pyramitela* (30.6%) and *T. pictum* (45.0%). Male spruce budworm moths were captured by at least 15 species of web-spinning spiders, whereas female budworm moths were captured by only 7 species of web spinners. At least 9 (18.4%) of the ensnared female moths were freshly emerged and gravid; most were captured by species of *Theridion*, i.e., *T. pictum* ($n = 5$), *T. murarium* Emerton ($n = 2$), and *T. frondeum* Hentz ($n = 1$). The *T. frondeum* capture was a male-female pair *in copula*; the gravid female moth was dead whereas the male was still alive when observed and collected.

G-tests indicated that significantly more ($P \leq 0.05$) male than female moths of the spruce budworm were captured by at least nine species of web-spinning spiders (Table 1). The overall species total was significantly biased ($P \leq 0.001$) toward capture of male spruce budworm moths. This differential mortality to male moths of the spruce budworm previously has not been discovered and reported.

Web surveys.—Because there were no significant differences in percentages of webs with budworm prey by survey method, we pooled the data from web-inventory sources. Over all spider species ($n = 11$ observed during surveys), study-site locations ($n = 6$), and observation dates ($n = 15$), the mean percentage of webs with spruce budworm moths was 15.99 ± 2.69 . Mean percentages of *F. pyramitela* and *T. pictum* webs with budworm prey were 19.49 ± 5.73 and 18.89 ± 3.56 , respectively. The arcsine transformed means for these two species were not significantly different (Wilcoxon 2-sample test, $Z = 1.38$, $P = 0.17$). Because percentages of webs with budworm prey ranged from 0-100 for some dates, the coefficients of variation were high over all species (166.77) and for both *F. pyramitela* (158.42) and *T. pictum* (92.47). Such variation was also evident when web percentages were plotted by observation date (Fig. 2) for these two species. Percentages of *T. pictum* webs with budworm moths peaked in early July and remained at a relatively high level ($\geq 20\%$); *F. pyramitela* webs declined sharply after an initial peak in mid-July.

Tree-web heights.—Tree height for *F. pyramitela* ranged from 0.6-5.5 m; web heights for this species ranged from 0.3-2.1 m. Correspondingly, tree heights for *T. pictum* ranged from 1.0-4.6 m; web heights ranged from 0.3-2.3 m. Tree- and web-height means were significantly different ($Z = 7.62$, tree; $Z = 4.31$, web) between species (Table 2); trees occupied by *T. pictum* were significantly taller ($P = 0.000$) and webs significantly higher ($P = 0.000$) than those of *F. pyramitela*. Mean relative web height was $> 60\%$ of tree height for both species; however, mean percentages were not significantly different ($Z = -1.05$, $P = 0.29$) between species (Table 2). Spearman's rank correlation coefficients indicated a greater degree of association between web and tree heights for *F. pyramitela* ($\rho = 0.58$, $P \leq 0.001$) than for *T. pictum* ($\rho = 0.24$, $P \leq 0.006$). However, relative web height

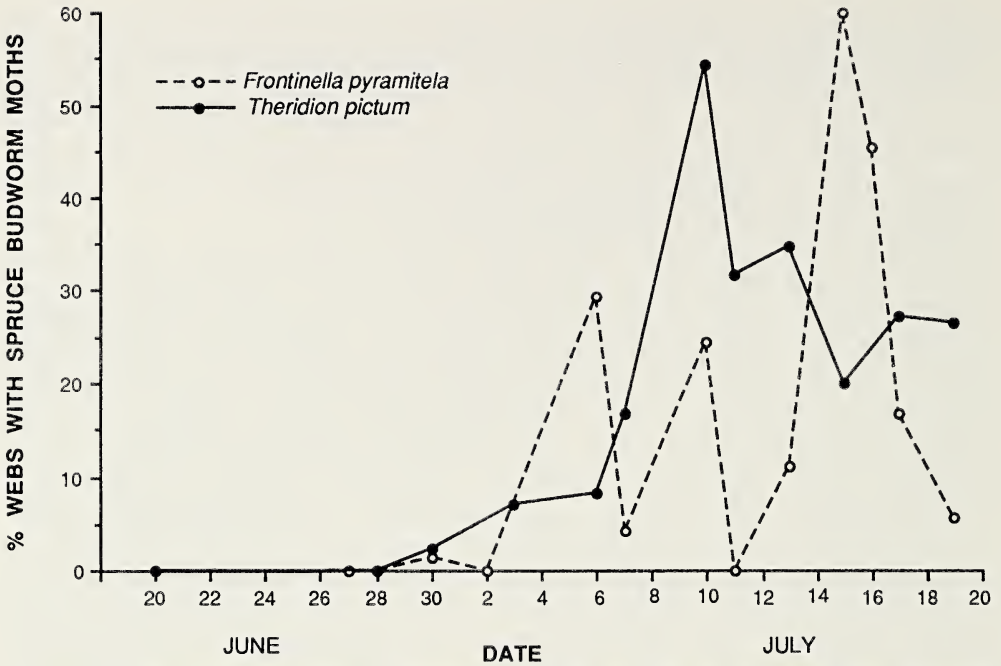


Figure 2.—Percentages of *Frontinella pyramitela* and *Theridion pictum* webs with spruce budworm moth prey by observation date; study sites and years combined.

was negatively correlated with tree height for *T. pictum* ($\rho = -0.53$, $P \leq 0.001$) and less so for *F. pyramitela* ($\rho = -0.13$, $P \leq 0.13$).

Next we considered tree, web, and relative web-height means for both species by prey-capture category (with, without budworm moth prey). For *F. pyramitela*, none of the means were significantly different between prey-capture category (Table 3); tree heights ($Z = -1.82$, $P = 0.07$), web heights ($Z = -1.24$, $P = 0.22$), relative web height ($Z = -0.74$, $P = 0.46$). For *T. pictum*, mean tree height was significantly taller ($Z = -2.58$, $P = 0.009$) for webs with budworm moths; however, web-height means did not differ significantly ($Z = 0.31$, $P = 0.76$) between prey-capture category. Mean relative web height was significantly less ($Z = 2.46$, $P = 0.01$) for *T. pictum* webs that captured spruce budworm moths (Table 3), possibly because tree height was significantly taller for these successful webs.

Kleptoparasites.—At least two species of kleptoparasites (Theridiidae) were observed and collected; *Argyrodes trigonum* (Hentz) from webs of *F. pyramitela* ($n = 4$), *T. pictum* ($n = 2$), and *Neoscona* sp. ($n = 1$); *Argyrodes fictitium* (Hentz) and *Argyrodes* sp. each from webs of *F. pyramitela* ($n = 2$). Specimens of *A.*

Table 2.—Comparisons of mean (\pm SE) tree, web, and relative web heights of *Frontinella pyramitela* and *Theridion pictum*, northeastern spruce-fir forests, Maine. Relative web height = web ht./tree ht. $\times 100$. Column means followed by different letters (a, b) are significantly different by Wilcoxon 2-sample test, $P = 0.05$ (SAS Institute 1985).

Spider species	n	Tree ht. (m)		Web ht. (m)		Rel. web ht. (m)	
		\bar{X}	(\pm SE)	\bar{X}	(\pm SE)	\bar{X}	(\pm SE)
<i>Frontinella pyramitela</i>	146	1.67a	0.05	1.06a	0.04	65.11a	1.76
<i>Theridion pictum</i>	134	2.14b	0.04	1.29b	0.03	62.61a	1.63

Table 3.—Comparisons of mean (\pm SE) tree, web, and relative web heights of *Frontinella pyramitela* and *Theridion pictum* by web-prey category, northeastern spruce-fir forests, Maine. Relative web height = web ht./tree ht. \times 100. Column means (within species) followed by different letters (a, b) are significantly different by Wilcoxon 2-sample test, $P = 0.05$ (SAS Institute 1985).

Spider species	n	Tree ht. (m)		Web ht. (m)		Rel. web ht. (m)	
		\bar{X}	(\pm SE)	\bar{X}	(\pm SE)	\bar{X}	(\pm SE)
<i>Frontinella pyramitela</i>							
with budworm moths	26	1.58a	0.19	0.98a	0.10	63.36a	3.31
without budworm moths	120	1.69a	0.05	1.08a	0.04	65.49a	2.02
<i>Theridion pictum</i>							
with budworm moths	83	2.22a	0.05	1.28a	0.04	59.18a	1.82
without budworm moths	51	2.02b	0.08	1.30a	0.05	68.18b	2.95

trigonum were collected at PEF, MED, T18, T19, and P14; *A. fictitium* and *Argyrodes* sp. were found only at MED. Most (72.7%, $n = 11$) of these kleptoparasites were associated with host-spider webs that had successfully captured male moths of the spruce budworm (1-3 moths/web). We did not observe *Argyrodes* spiders feeding directly on budworm prey.

DISCUSSION

Spider habitat associations.—The species of web-spinning spiders that we collected from understory balsam fir and spruce differ markedly from the terricolous spider fauna of Maine's spruce-fir forests (Jennings et al. 1988; Hilburn and Jennings 1988). However, many of the understory species also are known to inhabit crowns of mature trees. For example, *Araniella displicata* (Hentz), *Pityohyphantes costatus* (Hentz), *Dictyna phylax* Gertsch & Ivie, and *Theridion murarium* Emerton have been collected from crowns of dominant/codominant red spruce and balsam fir in Maine (Jennings and Collins 1987; Jennings and Dimond 1988). The orb weaver *Cyclosa conica* (Pallas) was found in foliage samples clipped from crowns of mature red spruce in Maine (Jennings and Dimond 1988); webs of this species also are found suspended between small trees in the understory. Species common to arboreal habitats of mature tree crowns and to small, understory tree strata of Maine's spruce-fir forests include *Araniella displicata*, *Dictyna phylax*, *Tetragnatha versicolor* Walckenaer, and *Theridion differens* Emerton.

Interestingly, the two species that we most commonly observed with budworm moth prey, *F. pyramitela* and *T. pictum*, apparently prefer the herb-shrub-small tree-zone in spruce-fir forests of Maine. Neither species has been taken in pitfall traps (Jennings et al. 1988; Hilburn and Jennings 1988), or among extensive foliage samples clipped from crowns of dominant/codominant red spruce (Jennings and Collins 1987), balsam fir, red and white spruce (Jennings and Dimond 1988), and hemlock (Jennings, unpublished data). In Maine's spruce-fir forests, webs of *F. pyramitela* most frequently are found on small trees and shrubs, and occasionally on low-growing forbs (≤ 0.3 m). Webs of *T. pictum* most commonly are found on small trees, less frequently on shrubs, and seldom on low-growing forbs in these forests.

Our data on web heights and relative web heights for *F. pyramitela* and *T. pictum* (Table 2) indicate a possible nonrandom selection of foraging patch by

both species, i.e., mean relative web height was $> 60\%$ of tree height for both species. And both species built their webs near branch apices where flying insects are apt to alight; webs of neither species were seldom observed within interiors of tree crowns. Selection of foraging patches near branch tips may favor predation on male moths of the spruce budworm because males "buzz" (i.e., slow, hovering flight) near the periphery of branches and near tree crowns (Sanders and Lucuik 1972; Greenbank et al. 1980). Other species of web-building spiders are known to make web-site selections based on prey abundance; see Riechert and Gillespie (1986) for a review on nonrandom selection of foraging patch by spiders.

Sex-biased predation.—Our observations over several years indicate that male moths of the spruce budworm are much more susceptible to predation by web-spinning spiders than female moths of this coniferous-tree defoliator, at least in the understory. We have no data on possible budworm-moth predation by web-spinning spiders that inhabit mature tree crowns; however, such predation is likely to be extensive, especially during budworm epidemics, because of the high densities of both spiders (Jennings and Collins 1987) and budworms (Morris 1955) found in crowns of mature conifers. For small coniferous trees in the understory, the current study confirms that significantly more ($P \leq 0.05$) male than female moths of the spruce budworm are captured by at least nine species of web-spinning spiders. The factors that cause and influence this differential mortality to male moths of the spruce budworm are unknown. We consider and discuss the following possibilities: 1) attraction of male moths of the spruce budworm to prey-mimicking pheromones emitted by spiders; 2) uneven densities and distributions of male-female moths in the understory; 3) accidental capture of male moths responding to "calling" female moths located near spider webs; 4) differences in male-female moth behavior; and 5) sexual differences in flight activities of spruce budworm moths. These factors are not necessarily independent, but may be interactive.

1) *Sex-pheromone mimicry*: There is mounting evidence that some spiders produce compounds that attract male moths (Hacker 1935; Eberhard 1977; Horton 1979; Yeargan 1988); the elicited responses are similar to the effects caused by sex pheromones of target prey species (review in Stowe 1986). Most observations of sex-pheromone mimicry concern species of araneid spiders that attract and capture only male moths; attracted Lepidoptera include species of Geometridae, Noctuidae, Pyralidae, and Olethreutidae (Stowe 1986), and Saturniidae (Horton 1979). Apparently, the ability to mimic sex pheromones of moths has evolved more than once (Stowe 1986), and the attractants emanate from the spiders (Eberhard 1977; Stowe 1986; Stowe et al. 1987) or from their webs (Horton 1979; Eberhard 1981). The preponderance of male budworm moths captured in spider webs in Maine suggests that sex-pheromone mimicry might be involved; however, field bioassays of male-moth attraction and olfactory-choice studies are needed to confirm such mimicry. Conversely, the capture of both male and female moths in some webs, and the apparent lack of prey specialization (i.e., captures included Homoptera, Diptera, Coleoptera, and Lepidoptera), lends minimal support to a sex-pheromone mimicry hypothesis. Additionally, several species of spiders of diverse families (Table 1) captured male moths of the spruce budworm; thus far, sex-pheromone mimicry by spiders has been confirmed for only a select few species, mostly Araneidae (Stowe 1986).

2) *Uneven prey densities*: Virtually nothing is known about the density and distribution of spruce budworm moths in the understory of spruce-fir forests. During outbreaks, small understory trees are defoliated by budworm larvae, and female moths deposit some eggs on needles of understory trees (Morris 1955; Jennings and Jones 1986). Most observations of spruce budworm moths concern dispersal flights and estimates of aerial densities of moths above the forest canopy (Greenbank et al. 1980). Measurements of moth densities within forest stands are extremely difficult because of intervening foliage layers, moth-flight activities, and differential responses of moth sexes to light traps (Greenbank et al. 1980). Despite these limitations, investigators have noted a markedly consistent 50% male: 50% female ratio for the budworm population in stands over the season (Miller 1963; Greenbank et al. 1980). However, exodus flights (emigration) from forest stands and mass invasions (immigration) of budworm moths into stands contain a high proportion of egg-carrying female moths (Greenbank et al. 1980). Because invading moths often drop to the ground, such invasions may affect moth densities in the understory. But in Maine, we never witnessed a mass invasion of moths at any study site. Although we cannot exclude possible unequal distributions and densities of moth sexes in the understory, we suspect that sexual differences in behavior and moth-flight activities were more influential in affecting sex-biased predation by web-spinning spiders.

3) *Accidental capture*: Sex-pheromone communication by the spruce budworm has received a great deal of attention from investigators (Sanders 1971, 1975; Sanders and Lucuik 1972, 1975), but the possible interrelationships between "calling" female moths and predators has not been studied. We suspect that the increased activities of male moths responding to sex pheromones greatly magnifies their chances of capture by web-spinning spiders. Spider webs *in situ* near "calling" female moths are apt to capture the most male moths; however, this hypothesis needs to be tested under field conditions. Female moths of the spruce budworm emerge from pupae in midafternoon (Sanders and Lucuik 1972), and remain sedentary near their place of emergence (Sanders 1975). The female moths start "calling" near dusk and continue calling throughout the night (Sanders 1971, 1975). Hence, female moths that emerge and emit sex pheromones near spider webs are apt to attract potential prey to these webs. The "buzzing" flight activity of male moths is continuous throughout the day but increases in intensity by mid-afternoon (Sanders and Lucuik 1972), and corresponds with the peak calling activity of female moths (Sanders 1971). Although we did not measure hourly capture rates for spider webs in Maine, we suspect that most moths were caught during the time of increased male-moth activity. We often observed spruce budworm moths flying into spider webs and being captured successfully by resident spiders during daylight hours; no observations were made at night.

Newly emerged, mated female moths of the spruce budworm also remain sedentary near their place of emergence (Sanders and Lucuik 1975) and call intermittently on successive days (Sanders and Lucuik 1972). Hence, spider webs *in situ* near such resident female moths may make multiple moth captures on successive days. This might explain why some webs captured male moths successfully during more than one observation period in Maine.

4) *Moth behavior*: Recent studies have shown that some insects are attracted to ultraviolet (UV) light reflected from spider webs (Craig and Bernard 1987);

however, such attraction has not been demonstrated for spider webs and spruce budworm moths in northeastern spruce-fir forests. The "buzzing" flights of male moths, from dawn until shortly after midnight (Greenbank et al. 1980) and near tree-crown peripheries within centimeters of branch tips (Greenbank 1973), suggests that: (a) male moths are active during the diurnal period of greatest light reflectance, and (b) male moths frequent zones where spider webs are common (i.e., near branch apices). Further, flying male moths of the spruce budworm are consistently photopositive to a discrete light source, whereas female moths generally are photonegative (Wellington 1948). These behavioral differences, coupled with heightened male moth-flight activity, might explain why male moths are more susceptible to predation by web-spinning spiders. Phototactic responses of male and female moths to UV-reflected light emanating from spider webs need to be tested in northeastern spruce-fir forests.

5) *Moth-flight activity*: Finally, greater male than female moth-flight activity probably is the factor that contributes most to spider predation on spruce budworm moths. Increased levels of potential prey activity should greatly influence the foraging success of "sit and wait" predators like some web-spinning spiders. Male moths of the spruce budworm are more active, both spatially and temporally, than female moths (Greenbank et al. 1980); such activity increases the likelihood of male-moth encounters with spider webs, and particularly with webs built near branch apices where male moth-flight activity is high. In laboratory experiments with spiders preying on aphids, Provencher and Coderre (1987) concluded that the most active prey, not necessarily the most abundant, will be the most captured. Because female moths of the spruce budworm generally remain sedentary, with few short, interbranch flights until 50% of their eggs are laid (Greenbank et al. 1980), female-moth encounters with spider webs initially are reduced. Males and spent females of the spruce budworm are more active than gravid females (Greenbank et al. 1980).

We conclude that the minimal flight activities of female moths after emergence reduces their susceptibility to spider predation—at least by web-spinning species. Conversely, the intensified flight activities of male moths—whether induced by sex-mimicking pheromones, moth sex pheromones, or UV-reflected light—increases their susceptibility to spider predation. Quantification of potential prey activities and their influences on spider predation need further investigation.

Web surveys.—The peaks in percentages of *F. pyramitela* and *T. pictum* webs with budworm prey (Fig. 2) generally coincide with peaks in pheromone-trap catches of spruce budworm moths in Maine's spruce-fir forests (Houseweart et al. 1981; Jennings et al. 1984). These results support our hypothesis that male-moth activity plays a significant role in predation by web-spinning spiders. Because pheromone traps measure male moth activity (Sanders 1971), daily trap catches may be useful for predicting captures of spruce budworm moths by web-spinning spiders. This assumes that predation by web-spinning spiders on spruce budworm moths is both density and activity dependent.

Future web surveys should take into account differences in web-residence times of host spiders; unoccupied webs are less likely to capture spruce budworm moths than occupied webs. During our sequential visits to tagged webs in Maine, we noted that as time progressed, *F. pyramitela* webs were more likely to be unoccupied than *T. pictum* webs. In New Jersey, Janetos (1984) observed a mean residence time of only 5.4 days for *F. pyramitela*. Scavenging of moth prey from

spider webs by ants and kleptoparasites also may confound survey results, i.e., underestimate predation by web-spinning spiders. Because some theridiid spiders feed on ants, ants may be more successful at removing budworm moths from sheetwebs of *F. pyramitela* than from tangle webs of *T. pictum*. Ants were included among the prey items removed from *T. pictum* webs in Maine.

Kleptoparasitism.—In addition to stealing prey from host spiders, Trail (1980) observed araneophagy by species of *Argyrodes*; the kleptoparasite attacks and kills the host spider (Wise 1982). Because of systematic destruction of several host spiders, Shear (1986) concluded that *A. fictilium* may be a specialist on *Frontinella communis* (Hentz) (= *F. pyramitela*). However, in Maine we found *A. trigonum* more commonly associated with *F. pyramitela* webs; only one specimen of *A. fictilium* was collected. Rypstra (1981) indicated that *Argyrodes* spiders may cause the host spider to move its web. We suspect that some of the web “abandonments” in Maine may be attributed to invasion and occupancy by *Argyrodes*, and possibly host-spider mortality induced by these kleptoparasites. For example, *Argyrodes* spiders were observed in 3 of 4 webs “abandoned” by *T. pictum* at MED. Both species of *Argyrodes* found during this study, *A. trigonum* and *A. fictilium*, have been recorded from Maine (Exline and Levi 1962).

Spider-budworm impacts.—What are the overall effects of spider predation on spruce budworm moths? Does sex-biased predation on male moths adversely affect the reproductive potential of the spruce budworm, and, consequently, population trend for the next generation? These and other questions need to be answered. This study shows that web-spinning spiders cause differential mortality to male moths of the spruce budworm; however, the consequences of such mortality on population dynamics of the budworm are unknown.

Predation by web-spinning spiders on male moths could hamper mating success and reproductive potential of the spruce budworm. Male moths of the spruce budworm mate only once, and female moths rarely mate more than once *per 24-h period* (Sanders 1975). Although males are capable of multiple matings (i.e., with more than one female), an increasing proportion of second and subsequent matings are infertile (Outram 1971). It follows then that significant mortality to male moths increases the likelihood that virgin female moths will remain unmated or be inseminated by “experienced” males with reduced fertility. Both unmated females and females from infertile matings of the spruce budworm lay few eggs (Outram 1971); hence, female oviposition success and reproductive potential are indirectly affected by male-moth survivorship. Likewise, predation on gravid female moths and moths *in copula*, as observed in this study, directly influences reproductive potential of the spruce budworm. Because of these potential impacts on spruce budworm reproduction, predation by spiders gains increased importance as a source of moth mortality. Additional studies are needed to assess age-interval survivorships of both predators and prey.

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This paper was in preparation when the junior co-author Mark W. Houseweart died unexpectedly. Although inadequate, this paper is dedicated as a memorial to his acute observational abilities, high standards of academic excellence, and superior research performance. Any errors of data analyses and interpretation are my own (D.T.J.).

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**SPECTRAL SENSITIVITIES OF PHOTORECEPTORS
IN THE OCELLI OF THE TARANTULA
APHONOPELMA CHALCODES (ARANEAE, THERAPHOSIDAE)**

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ABSTRACT

Spectral sensitivities of primary and secondary eyes in the Theraphosid spider, *Aphonopelma chalcodes* Chamberlin, were investigated by recording intracellular receptor potentials from single photoreceptors. The responses of all cells were graded depolarizations, monophasic in waveform. All cells showed dual spectral sensitivities, with a primary peak near 500 nm and a secondary peak in the near ultraviolet at 370 nm. The 500 nm peaks were fit well by a Dartnall nomogram.

Spectral sensitivity curves were similar under both dark and light adaptation suggesting the presence of a single photopigment. Intensity-response functions with *white* light showed sensitivity differences between primary and secondary eyes. Secondary eyes had greater sensitivity ranges and smaller slope coefficients showing them to be more sensitive than primary eyes.

INTRODUCTION

Differing spectral sensitivities of visual cells are of considerable interest because they are an essential condition for wavelength discriminations in visual behavior. In several species of spider, multiple and differentiable sensitivities have been reported to both visible and to near-ultraviolet spectral regions: in the wolf spider, *Lycosa* (DeVoe, Small and Zvargulis 1969; DeVoe 1972); in the jumping spider, *Phidippus* (DeVoe 1975), in *Menemerus* (Yamashita and Tateda 1976, 1981), in *Plexippus* (Blest, Hardie, McIntyre and Williams 1981); and in *Argiope* (Yamashita and Tateda 1976, 1978, 1981; Tiedemann, Ventura and Ades 1986).

In this paper, we report spectral sensitivities from the visual cells of ocelli in another spider, the New World Tarantula *Aphonopelma chalcodes* Chamberlin. The arrangement of ocelli consisting of primary and secondary eyes is shown in Figure 1. Spectral sensitivities were measured from single photoreceptor cells in each of the ocelli by means of intracellular recording. Both intensity-response functions and action spectra were derived from the basic recordings. Comparative evaluations were made among the several ocelli; comparisons were also drawn between *Aphonopelma* and other arthropods.

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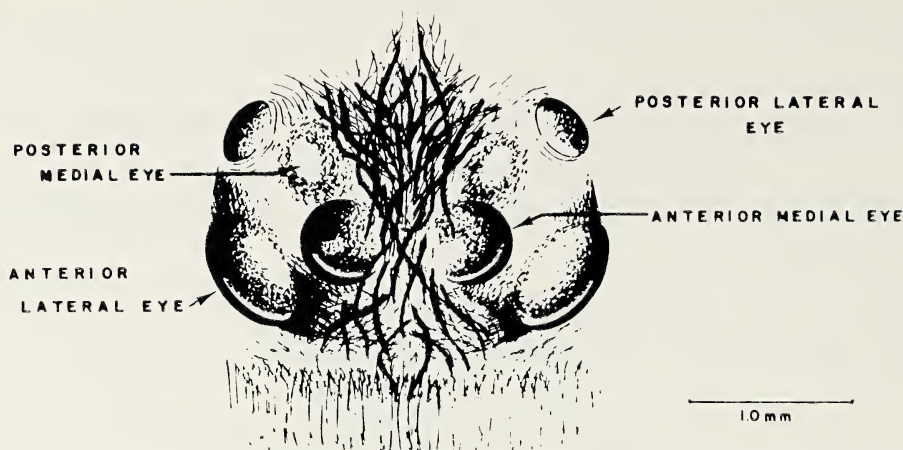


Figure 1.—Cormorus of *Aphonopelma chalcodes*. The eight eyes are arranged on the cormorus of the anterior portion of the cephalothorax as four sets of paired eyes: the *primary* Anterior Medial Eyes (AME); and the *secondary* Anterior Lateral Eyes (ALE), Posterior Medial Eyes (PME), and Posterior Lateral Eyes (PLE).

METHODS

Experimental animals.—Thirty-one female spiders were purchased from commercial sources. Their weights and pubescence were suggestive of pre-adult instars.

Preparation.—After an experimental animal was rendered tractable with carbon dioxide, the legs and the abdomen were cut off near the cephalothorax. The isolated cephalothorax was pinned dorsal surface down to a cork block in an especially constructed lucite chamber, and then immersed in spider saline solution (Rathmayer 1965). The paturons of the chelicerae and endites were removed, revealing the ocelli attached to the hemocoelic surface of the cormorus. The optic nerves were left intact. Access to the ocelli then required only minor dissection of the musculature. A 1.0 - 1.5% w/w solution of Fungal Type VI protease in saline was applied to the ocelli for one to three minutes to soften the ocellar capsule and to allow easy penetration by the electrodes.

Optical system.—A two-channel optical system was employed. One channel served for monochromatic stimulation, while the other provided light for chromatic adaptation. In Channel 1, the light from a 150W xenon arc lamp was passed through a monochromator, collimated, and focused on the tip of an ultraviolet, light-conducting, fiber-optic guide. Light intensity was controlled by neutral density wedges continuously variable over 6.65 optical density units. Light duration was controlled by an electrically operated solenoid with attached flag. An auxiliary shutter was placed in the light path of Channel 1 and used during chromatic adaptation. In Channel 2, light at either 546 nm or 365 nm from a mercury lamp was isolated by using appropriate cut-off filters; the beam was then directed onto a beam splitter in the path of Channel 1, and the combined lights were focused on the tip of the fiber optic.

The stimulus and chromatic adaptation lights were calibrated using a black-body thermopile with attached microvoltmeter. All light fluxes were specified in log photons $\cdot \text{cm}^{-2} \cdot \text{s}^{-1}$ emergent from the light-guide tip.

Recording system.—Intracellular potentials were recorded from single photoreceptor cells by means of glass micropipette electrodes filled with 3M KCl. The electrodes had measured tip resistances in the range 60–80 megohms. All recordings were conventional. Permanent records were captured on film from which the measurements were made.

Experimental protocol.—Once a cell was penetrated and stable at a membrane potential between -30 mV and -40 mV, it was allowed to dark adapt for 30 min. Rapid spectral sensitivity scans, consisting of 100 ms flashes of monochromatic light over a 3 log unit range, were then made. For all spectral scans, low criterion amplitudes of 4 mV were elicited to avoid light adaptation of the preparation. Scans were done in balanced order using 370 nm and 520 nm flashes as control wavelengths. The first four flashes of each scan were control flashes followed by test flashes that in turn were interrupted by additional control flashes every fifth flash. Spectral scans spanned the spectrum from 360 nm to 640 nm, in 20 nm increments, for a total of 23 flashes per complete scan. Each scan was followed by an 11-point intensity-response series at the two control wavelengths. With interflash interval at 40 s, a complete scan took from 40 to 50 min from the time of initial impalement. Cells were also scanned under chromatic adaptation in order to determine visible and ultraviolet contributions. Such experiments were begun with a dark-adapted scan that was followed by scans under chromatic adaptation at 365 nm or 546 nm. These chromatic lights were of an intensity that elicited dark-adapted potentials of approximately 50% saturation amplitude.

RESULTS

Receptor potential.—Intracellular receptor potentials consisted of graded depolarizations to light; no regenerative responses were observed. Figure 2 shows the receptor potential of an anterior lateral eye (ALE) to monochromatic light flashes at 520 nm for three durations. These responses are typical of responses recorded from all cells. The response waveform was characterized by an initial transient depolarization that occurred to light onset, followed by a slow return of the membrane potential to its resting level. The form of the response is seen most clearly to the 100 ms flashes of Fig. 2. The transient there forms a peak which then decays slowly to the baseline from its maximum value. To longer stimulus flashes (500 and 900 ms), peak responses show longer time courses that merge with overall response decays. Even to flashes longer than 900 ms, response decays were gradual and never showed abrupt returns to baseline upon flash cessation (cf. DeVoe 1972, 1975). No differences in waveform were observed in the responses to different wavelengths of light. Occasional, irregular, transient variations in potential (*bumps*), associated with less intense lights of long duration were seen. They were similar to those reported in *Limulus* by Yeandle (1958) and probably result from membrane responses to single photon absorptions.

Peak response amplitudes varied directly as the intensity of light, although the period of depolarization was longer for longer flashes. The latency of response was inversely related to light intensity.

Intensity-response functions.—Figure 3 shows the functional relationship between response peak amplitude and light intensity. The responses were recorded to *white* light which was attenuated over a seven log unit range. The curve for the

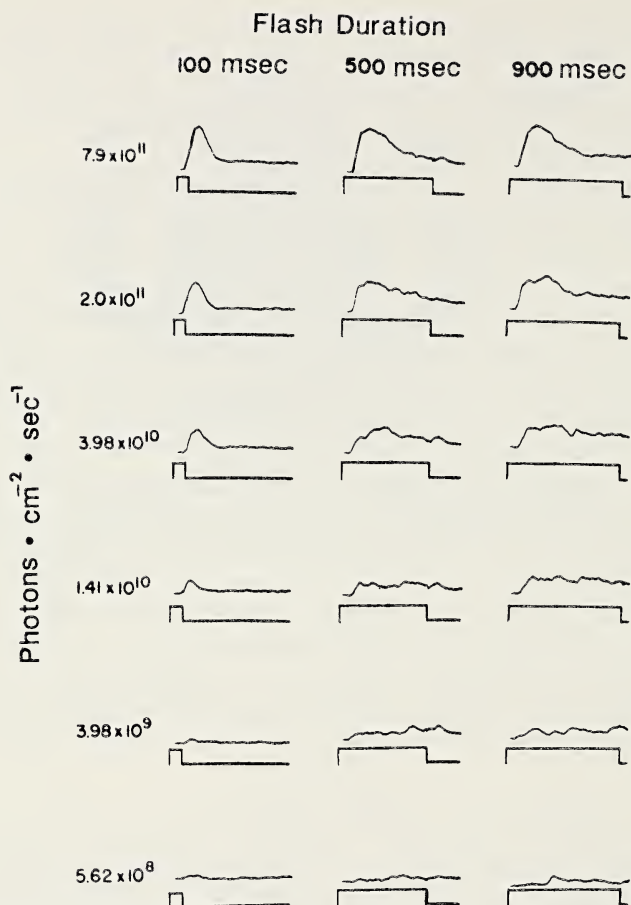


Figure 2.—Responses of ALE to monochromatic light of 520 nm. Flash durations of 100, 500, and 900 ms are listed above each column. Light intensities over a three log unit range are listed as ordinal values. An indicator for light onset and offset is shown beneath each receptor potential; its vertical displacement measures a calibrated 10.0 mV.

primary anterior median eye (AME) consists of 16 points, while the curve for a secondary anterior lateral eye (ALE) consists of 20 points. These points were fit by the Michaelis-Menten equation of format: $V/V_{\max} = I^n / (I^n + k)$, where V/V_{\max} is the normalized intracellular response potential, k is the intensity of light required for one-half maximum response potential, and I is an increment of light intensity (Naka and Rushton 1966; Stryer 1988:189). When comparing the two curves, the AME curve shows a greater slope coefficient than the ALE curve: the value of n is 0.71 for AME, and 0.55 for ALE. The slope differences between the two curves indicate a one log unit stimulus intensity difference at the one-half maximum response potential point in Fig. 3. This horizontal separation reflects differences in sensitivity for the two classes of eyes (Glantz 1971). The ALE cells possess an overall sensitivity advantage for dimmer lights, whereas this difference is nearly gone at about -1.5 log units where the curves begin to overlap. The linear range of sensitivity for AME is 1.5 log units, while the range for the corresponding ALE curve is 3.0 log units.

Figure 4 displays sample intensity-response functions for several sample wavelengths that plot peak amplitudes of response against light intensities for

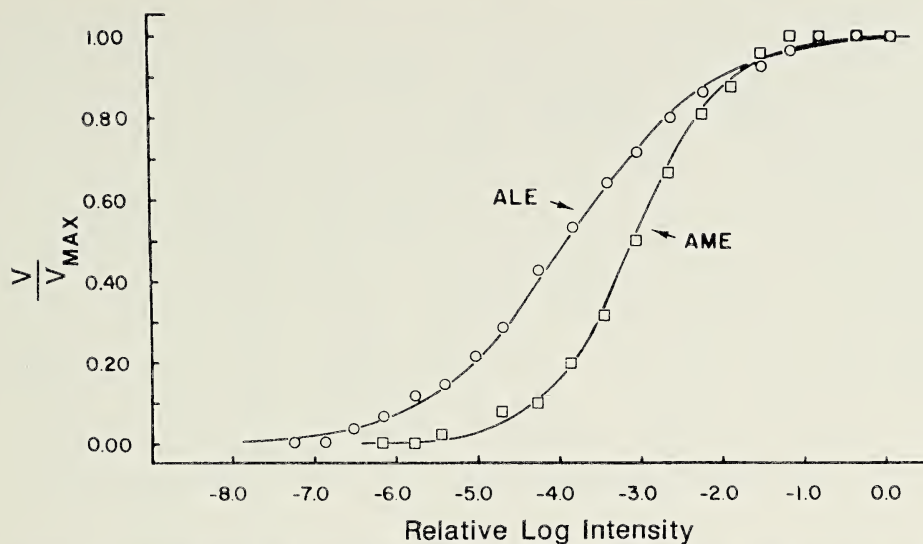


Figure 3.—Intensity-response functions to *white* light for AME and ALE cells. Amplitudes were normalized and plotted against relative log light intensity. Each point is a mean for three cells with standard deviations not larger than ± 0.05 .

AME and ALE cells. Within each kind of eye, intensity-response functions are remarkably linear, and for each eye, alike in slope regardless of stimulus wavelength. The two sets of curves differ however in their degree of slope (see Discussion).

Spectral sensitivity.—Reciprocal values of photon flux necessary to elicit criterion responses of 4.0 mV at each stimulus wavelength formed the spectral sensitivity curves. Responses of this amplitude permitted use of dim lights that did not result in appreciable light-adaptation of the cells. Action spectra for dark-adapted cells of AMEs, ALEs, PMEs, and PLEs are shown in Fig. 5. The cells of both primary and secondary eyes possess spectral sensitivity curves that are virtually identical in shape. All curves possess major sensitivity peaks near 500 nm as well as peaks of lower sensitivity in the near ultraviolet at 370 nm. Points for the longer wavelengths agree well with the Dartnall (1953) nomogram for a vitamin A_1 -based photopigment peaking at 500 nm.

The measured range of wavelength sensitivity for all cells lies between 350 and 640 nm. The logarithmic difference between the sensitivity peak in the 440 nm to 640 nm range, and the sensitivity peak in the near ultraviolet, 350 nm to 400 nm, varied from 0.60 to 0.70 log unit. The overall range of sensitivity within the experimental scan, from the most sensitive point near 500 nm and the least sensitive point at 640 nm, measured 2.5 log units for all eyes.

Chromatic adaptation.—To isolate the visible or near-ultraviolet peaks, stable cells in both AME and ALE were adapted with monochromatic lights of 365 nm or 546 nm (see Methods). A representative cell is shown for each group in Figs. 6 and 7. For all light-adapted cells, overall sensitivities were reduced relative to their dark-adaptive states, but the shapes of the curves remained virtually the same. Accompanying the cells' progressive reduction in sensitivity, when adapted to 365 nm or 546 nm light, was a decrease in sensitivity difference between longer wavelength and near ultraviolet peaks. In dark-adaptation, this sensitivity

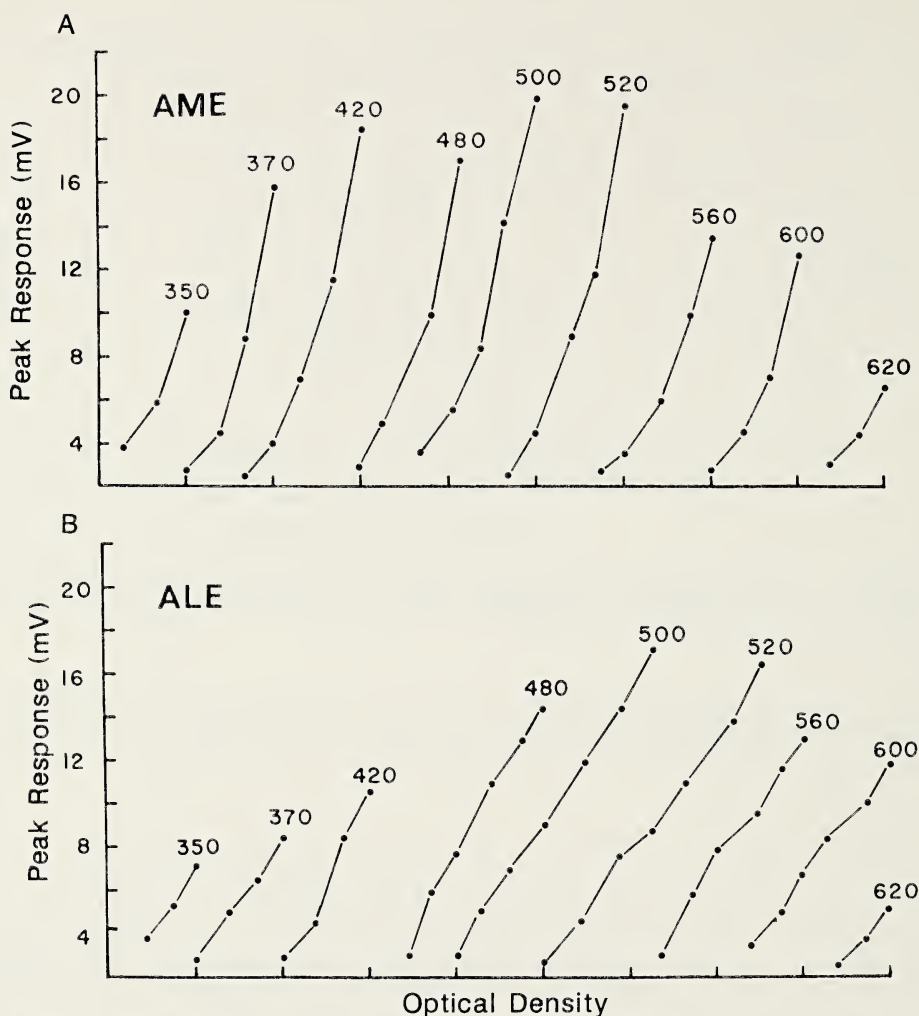


Figure 4.—A. Selected intensity-response functions for an AME cell. Response amplitude is plotted against optical density attenuation indicated as unit values on the abscissa; the response curves are separated for clarity. B. Intensity-response functions for an ALE cell is displayed as in A.

difference was 0.70 log unit, which then decreased to 0.56 log unit under chromatic adaptation to 365 nm light and to 0.35 log unit under 546 nm light.

DISCUSSION

Although primary and secondary eyes of *Aphonopelma chalcodes* display anatomical dimorphism, no functional differences were found between the two sets of eyes for two of three parameters studied. Both intracellular responses, and the spectral sensitivity functions derived from them, showed remarkable similarities. Time courses and general shapes of the waveforms did not differ between the two types of ocelli; neither did spectral sensitivity functions differ in their regions of peak sensitivity. Both primary (AME) and secondary ocelli (ALE, PME, and PLE) showed sensitivity peaks near 500 nm, with prominent peaks in

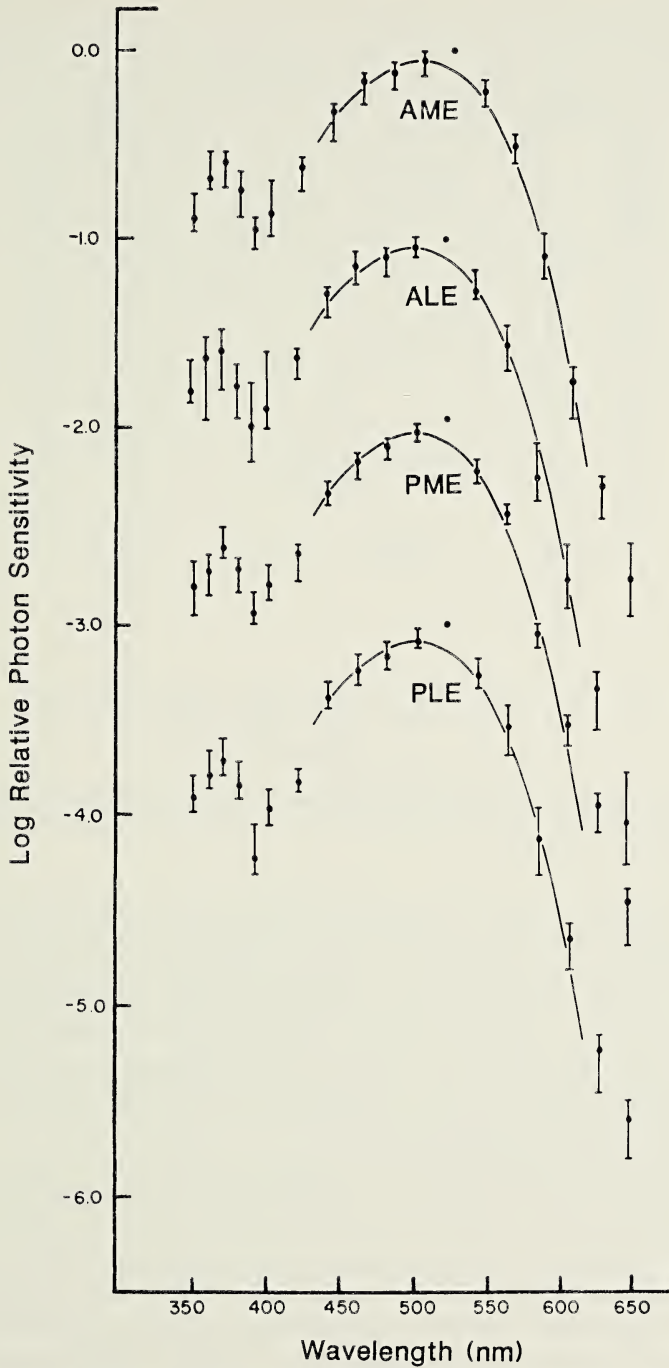


Figure 5.—Spectral sensitivity curves for AME, ALE, PME, and PLE cells. The curves are displaced vertically for clarity. Data points for each curve are mean spectral sensitivities for 12 cells normalized at 520 nm to a log relative photon sensitivity of 0.0. Vertical lines are ranges of the data points. The solid lines are derived from the nomogram of Dartnall (1953) for an A_1 photopigment absorbing maximally at 500 nm. Ordinal values related to each curve are sensitivity values derived from $-\log$ relative photon fluxes that produce 4 mV responses by 100 ms light flashes at the stimulus wavelengths in nanometers (nm) indicated on the abscissa. Mean light intensity at 500 nm was 1.2×10^9 photons \cdot cm $^{-2}$ \cdot s $^{-1}$.

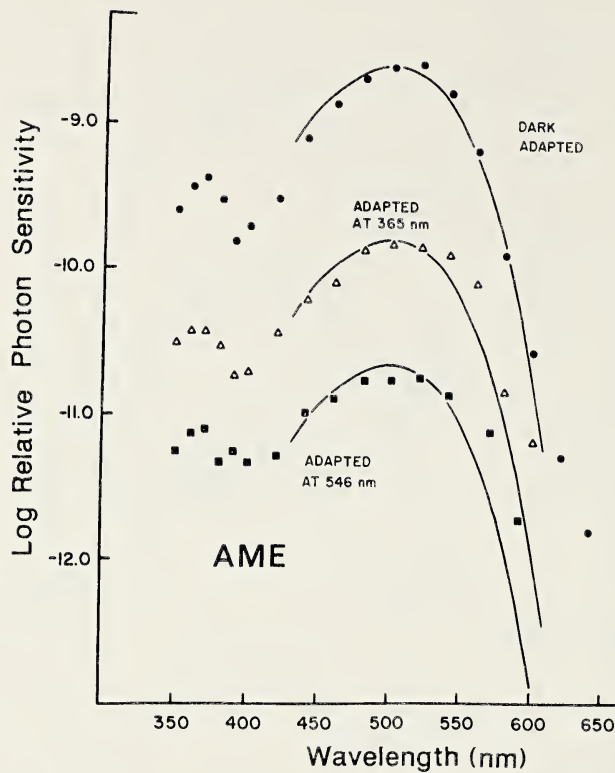


Figure 6.—Spectral sensitivity curves for a dark- and chromatically light-adapted AME cell. Solid line is derived from the Dartnall nomogram as in Fig. 5. The actual placement of individual curves derives from changes in adaptation.

the near ultraviolet at 370 nm. There was, however, a difference with respect to overall sensitivity to light. As shown in Fig. 3, the intensity-response function for the secondary ocellus ALE, showed a shallower slope coefficient (0.55) than did the function for the primary ocellus AME (0.71). The differing slopes with wavelength as a parameter can be seen in Fig. 4. Secondary ocelli are apparently able to efficiently integrate photon absorptions over a more extensive range of light intensities than do primary ocelli.

Receptor potentials and waveforms.—Receptor potentials of tarantula photoreceptors to flashes of light consist of smoothly graded depolarizations. The graded changes in membrane potential are consistent with intracellular receptor potentials recorded from other arthropod eyes and are of the same polarity (DeVoe 1975; Bruno, Mote and Goldsmith 1973). There were transient decreases in membrane potentials to light onset followed by slow restorations to initial resting levels, even with flashes longer than 100 ms. These waveforms are in contrast to those reported for wolf spider by DeVoe (1972), where prolonged flashes of light produced marked OFF responses.

Spectral sensitivity.—All photoreceptor potentials recorded from cells in AME, ALE, PLE, and PME showed a common sensitivity peak in the visible wavelengths at 500 nm, together with a lesser peak at 370 nm in the near ultraviolet, the two peaks differing in sensitivity by about 0.7 log unit. These results are in close company with the dual sensitivities that are maximum at 360-

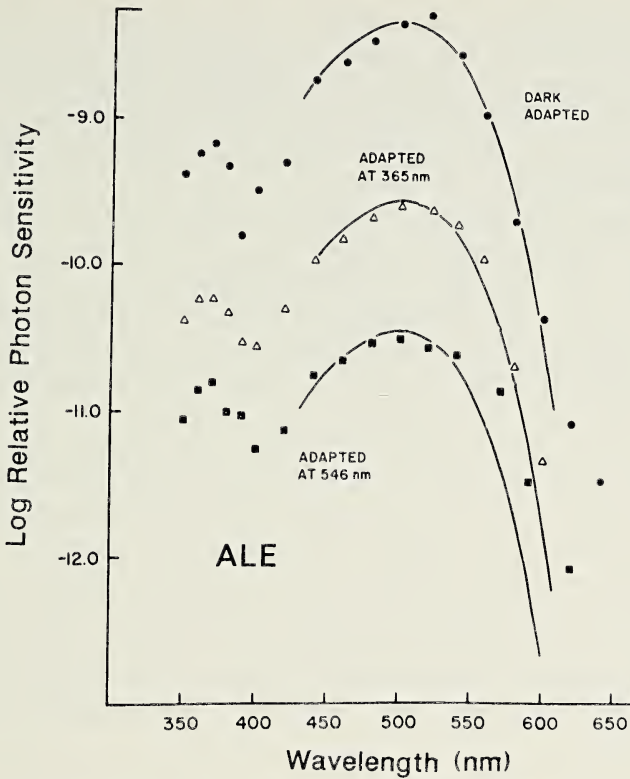


Figure 7.—Spectral sensitivity curves for a dark- and chromatically light-adapted ALE cell. See legend to Figure 6.

370 nm and at 510 nm in the principal eyes and in the anterior lateral eyes in wolf spider (DeVoe 1972). Principal eyes of the orb-weavers, *Agiopie bruennichii* and *Agiopie amoena*, on the other hand, have three types of receptor cells with maximum sensitivities at 360 nm, 480-500 nm, and 540 nm. Posterior lateral eyes for these same spiders show similar peak sensitivities (Yamashita 1985). In general, principal and secondary eyes of *Salicidae* and *Lycosidae*, when assessed intracellularly, have cells that correspond to *Aphonopelma* (cf. Yamashita 1985, tables 1 and 2). The excellent fit of the data points in Fig. 5 by the Dartnall nomogram supports the idea that measured spectral sensitivities most likely derive from a single vitamin A₁-based photopigment (Dartnall 1953). In further support of this idea is the fact that chromatic adaptations with 365 nm and 546 nm lights produced no differential effects. There is also evidence that parametric changes in stimulus intensity can result in matched waveforms regardless of wavelength, an argument for simple intensity effects but not one that reflects spectral changes. From all these lines of evidence, it is unlikely that *Aphonopelma* possess any ability to discriminate wavelengths.

Information over optic nerves in most animals is coded as regenerative action potentials. That is normally not the case in wolf spiders (DeVoe 1972) nor is it for *Aphonopelma* (personal observations). Photoreceptor excitation is conducted to the supraesophageal ganglion in the form of decremting graded potentials. Although rare, nonregenerative neural activity is known to occur in other arthropod visual systems (Ionnides and Walcott 1971; Shaw 1972). The quality of

information transmitted to optic centers in this fashion must of necessity be primitive. *Aphonopelma* may therefore respond simply to the fundamental dimension of ambient light intensity. Complexities of wavelength discrimination and contour perception are apparently not involved, for the visual system here is functionally homogeneous and shows none of the response complexities seen in color discriminating eyes.

Ocellar structure and function.—Similar to many spiders, secondary ocelli in *Aphonopelma* possess tapeta. Tapeta provide a mechanism for lightpath doubling; they lie very close to the rhabdomeres so that reflected light immediately retraverses these photopigment-bearing cells (Land 1972). There are no tapeta in primary ocelli, and light traversing these rhabdomeres is absorbed by the heavily pigmented capsule of the ocellus after a single passage. When intensity-response functions for primary and secondary ocelli are superimposed, these curves reveal that at equivalent lights, and also for less intense lights, responses of secondary ocelli are larger than those of primary ocelli. This finding is consistent with the idea that secondary ocelli and associated structures have evolved as detectors of dim lights. The functions for secondary ocelli are less steep than those for primary ocelli, and this property suggests a more efficient response range for a given intensity range of light input. There appears to be in these structures a simple duplex arrangement that accounts for a greater range of light sensitivity than would otherwise be possible, an arrangement that performs for *Aphonopelma* what rods and cones do in the intensity domain for the vertebrate retina.

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THE HARVESTMAN FAMILY PHALANGODIDAE. 2. THE NEW GENUS, *MICROCINA* (OPILIONES, LANIATORES)

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ABSTRACT

A new phalangodid genus, *Microcina*, is described to accommodate *Sitalcina tiburona* Briggs and Hom and five new species (*edgwoodensis*, *homi*, *jungi*, *leei*, and *lumi*). The species are diagnosed and illustrated and their relationships hypothesized.

The six species of *Microcina*, known only from the San Francisco Bay region, are all paedomorphs restricted to xeric habitats. Two species groups are present: the first (*tiburona*) is characterized by a unique form of sexual dimorphism (males have enlarged eye tubercles); the second (*homi*) by unique male genitalia, structurally intermediate between *Calicina* and the remaining Nearctic phalangodid genera.

INTRODUCTION

The phalangodid genus *Sitalcina*, established by Banks (1911) for *Sitalces californicus* Banks, was revised and greatly enlarged by Briggs (1968). In our recent study (Ubick and Briggs 1989), *Sitalcina* was shown to be polyphyletic and most of the species were transferred to a newly established genus, *Calicina*. At that time three species remained unplaced. One of these species, *Sitalcina tiburona* Briggs and Hom, represents yet another new genus, *Microcina*, the focus of this paper.

This study is based on the examination of 140 specimens, almost all from the collection of TSB and now deposited in the California Academy of Sciences; additional material was borrowed from and is deposited at the American Museum of Natural History (New York). The specimens were collected by the authors and the following persons: Lee Cheng, C. Fox, A. Gray, Kevin Hom, Albert Jung, Jason Lee, Vincent F. Lee, Bill Lum, Toshiro Ohsumi, and Ken Wang. The specimens were prepared and examined as in Ubick and Briggs (1989). The species descriptions are brief, partly because character states shared at higher levels (genus and species group) are not repeated. More important is the apparent absence of significant intraspecific variation in *Microcina* for the characters examined. Some variation in size has been recorded and is given in Table 1. There is also little interspecific variation between the members of the *tiburona* group and no characters have been found to reliably distinguish the females. All specimen measurements are in mm.

Table 1.—Measurements (in mm) of *Microcina* species giving ranges, means, and standard deviations. Abbreviations are TBL = total body length, SL = scute length, SW = scute width, LIIL = leg II length, ETL = eye tubercle length, ETW = eye tubercle width.

Species	Sex	N	TBL	SL	SW	LIIL	ETL	ETW
<i>homi</i>	m	13	0.82-1.00	0.55-0.72	0.58-0.69	1.40-1.90	0.13-0.18	0.12-0.18
			0.888±0.053	0.625±0.044	0.626±0.035	1.594±0.132	0.145±0.013	0.139±0.016
	f	19	0.79-1.05	0.55-0.74	0.56-0.78	1.51-1.92	0.12-0.18	0.13-0.18
			0.904±0.075	0.640±0.049	0.661±0.067	1.651±0.133	0.145±0.015	0.150±0.015
<i>tiburona</i>	m	17	0.97-1.21	0.76-0.87	0.69-0.85	1.90-2.44	0.22-0.28	0.24-0.33
			1.095±0.060	0.810±0.035	0.759±0.041	2.078±0.144	0.251±0.017	0.274±0.021
	f	13	0.97-1.22	0.67-0.80	0.71-0.85	1.82-2.18	0.18-0.21	0.18-0.23
			1.074±0.062	0.765±0.035	0.779±0.041	1.984±0.133	0.187±0.012	0.211±0.013
<i>leei</i>	m	3	0.87-1.10	0.64-0.70	0.59-0.67	1.74-1.85	0.18-0.19	0.21-0.23
			0.973±0.117	0.677±0.032	0.637±0.042	1.797±0.055	0.183±0.006	0.217±0.012
	f	3	0.80-0.97	0.63-0.69	0.57-0.69	1.60-1.70	0.12-0.15	0.15-0.18
			0.863±0.093	0.650±0.035	0.620±0.062	1.663±0.055	0.140±0.017	0.167±0.015
<i>lumi</i>	m	5	0.97-1.10	0.72-0.79	0.68-0.72	1.69-1.87	0.18-0.26	0.23-0.28
			1.040±0.054	0.760±0.029	0.712±0.018	1.804±0.074	0.224±0.029	0.250±0.021
	f	4	0.95-1.18	0.64-0.72	0.68-0.77	1.77-1.87	0.13-0.15	0.15-0.18
			1.070±0.112	0.675±0.037	0.720±0.042	1.815±0.042	0.145±0.012	0.170±0.014
<i>jungi</i>	m	4	1.05-1.20	0.77-0.88	0.73-0.83	1.97-2.13	0.21-0.26	0.26-0.31
			1.107±0.065	0.847±0.052	0.785±0.042	2.082±0.076	0.232±0.021	0.280±0.022
	f	2	0.97-1.10	0.75-0.77	0.78-0.80	1.93-2.00	0.17-0.18	0.18-0.19
			1.035±0.092	0.760±0.014	0.790±0.014	1.965±0.050	0.175±0.007	0.185±0.007
<i>edge-woodensis</i>	m	3	0.90-0.97	0.67-0.70	0.62-0.70	1.50-1.87	0.18-0.21	0.22-0.26
			0.940±0.036	0.683±0.015	0.650±0.043	1.733±0.203	0.193±0.015	0.247±0.023

Microcina, new genus

Sitalcina: Briggs and Hom 1966. Briggs 1968 (in part).

Diagnosis.—Species of *Microcina* appear to be unique among the Nearctic Phalangodidae in having an areolate body cuticle (Fig. 1). They are further distinguished from other phalangodids with reduced tarsal counts (3-4-4-4) in having a penis with a folding glans and an ovipositor cuticle completely covered with microspines.

Type species.—*Sitalcina tiburona* Briggs and Hom, 1966.

Etymology.—The generic name is a contraction of micro and *Sitalcina*, referring to the small size of the species, and is feminine in gender.

Description.—Color of body pale orange; appendages yellowish white. Abdominal integument (of preserved specimens) somewhat transparent; irregular white masses visible beneath cuticle. Body length 0.8 to 1.2 mm. Carapace cuticle with honeycomb network of ridges (areolate); flattened tubercles present in cephalic region. Tergites with posterior margins tuberculate (*homi* group) or smooth (*tiburona* group). Eye tubercle low and rounded (enlarged in males of the *tiburona* group); cornea and retina absent. Anterior margin of carapace with 1 pair of anterior tubercles; ozopores lateral. Venter similarly sculptured as dorsum. Palp with typical number and arrangement of megaspines: tarsus and tibia with two pairs each, patella with one (mesal), and femur with one mesoapical and three ectobasal. Tarsal count 3-4-4-4. Ovipositor surface with prominent ridges; completely covered with microspines; with 7 pairs of apical setae; setae apically hooked. Penis with folding glans, which also telescopes in the *homi* group. Stylus curved, spinelike; basally surrounded by a pair of lobes. Ventral plate rounded

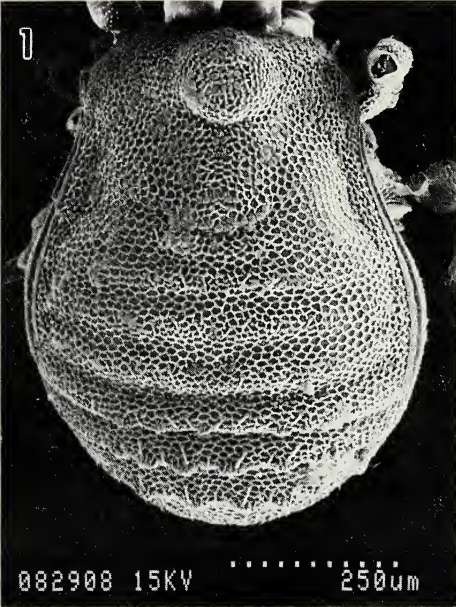


Figure 1.—*Microcina homi*, male topotype, dorsal view.

apically, with 1 pair of stout, lateral setae and 3-4 pairs of smaller, ventral setae; *homi* group with additional 2 pairs of lateral setae.

Natural history.—All species are winter active paedomorphs known only from xeric habitats.

Distribution.—The San Francisco Bay region of California.

Species.—The six species, representing two species groups, can be separated by the following key. No characters were found to distinguish females of the *tiburona* group.

KEY TO SPECIES OF *MICROCINA*

1. Male eye tubercle subequal to that of female. Penis stylus telescopes during expansion (Figs. 16-18); oviposter setae with simple tips (Fig. 10) (*homi* group) *homi*
 Male eye tubercle distinctly larger than that of female (Figs. 2-5). Stylus does not telescope during expansion (Figs. 21-33); ovipositor setae with trifurcate tips (Figs. 12, 13) (*tiburona* group) ..2
2. Penis apical lobes pointed, stylus slightly sinuous (Figs. 24, 32).3
 Apical lobes rounded, stylus strongly sinuous (Figs. 22, 26, 30).4
3. Apical lobes narrow, surface lightly fringed (Fig. 32).*edgewoodensis*
 Apical lobes wide, surface strongly fringed (Fig. 24).*leei*
4. Penis substylar knob rounded (Fig. 26).*lumi*
 Substylar knob angular (Figs. 22, 30).5
5. Apical lobes with serrate ventral margin (Fig. 22)*tiburona*
 Apical lobes with smooth ventral margin (Fig. 30).*jungi*

The *homi* species group

Diagnosis.—The single species representing this group, unlike other *Microcina*, has tubercles on the posterior tergite margins (Fig. 1). Males are unique among the Nearctic Phalangodidae in having a glans which both unfolds and telescopes during expansion (Figs. 14, 15, 18). Males are also distinguished from other *Microcina* in lacking enlarged eye tubercles (Fig. 1), in having the ventral plate with both ventral and lateral setal series (Fig. 17), in having a glans with apical lobes bearing stout fringe flaps (Fig. 7), and in lacking a substylar knob and dorsal flap on the glans (Figs. 6). Females have ovipositor setae with simple tips (Fig. 10).

Distribution.—Known only from Santa Clara County (Fig. 34).

Microcina homi, new species

Figs. 1, 6, 7, 10, 11, 14-20, 34.

Sitalcina minor Briggs and Hom, 1966:263 (in part, all individuals from Santa Clara County).

Diagnosis.—Same as for species group.

Etymology.—Named after Kevin Hom, collector of these and numerous other rare and unusual phalangodids.

Description.—*Male (Holotype)*: Total body length, 0.85. Scute length, 0.55; width, 0.61. Eye tubercle length, 0.14; width, 0.12. Leg II length, 1.40. Penis as illustrated (Figs. 6, 7, 14-20).

Female: Total body length, 0.88. Scute length, 0.60; width, 0.62. Eye tubercle length, 0.12; width, 0.13. Leg II length, 1.60. Ovipositor as illustrated (Figs. 10, 11).

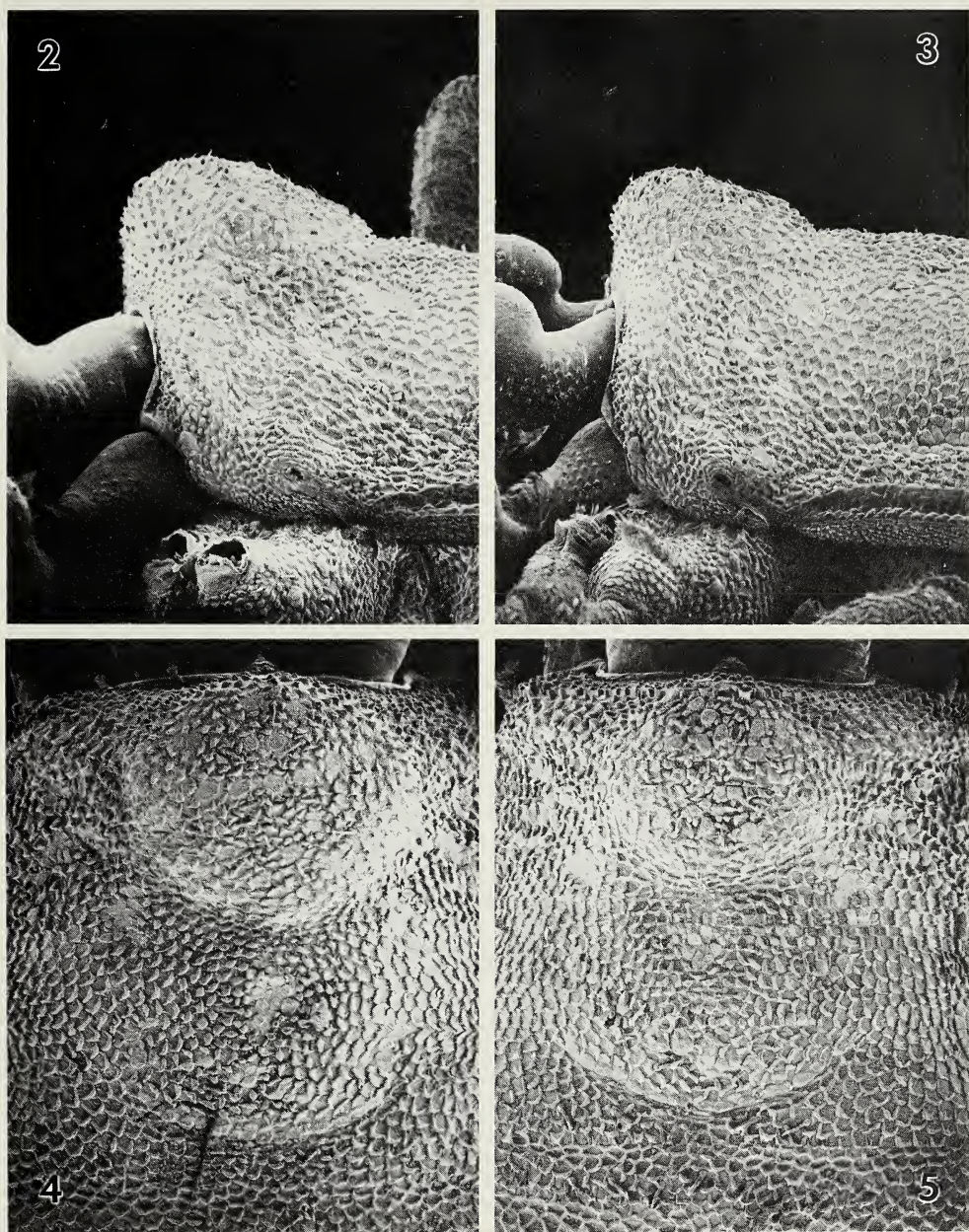
Natural history.—Known only from grassland habitats. Specimens from Santa Teresa Park were collected beneath Franciscan sandstone; all others are from serpentine. This species is fully sympatric with *Calicina serpentinea* (Briggs and Hom) and at one locality (0.9 mi. S Junction of Silver Creek and San Felipe Roads) with *Microcina jungi*, new species.

Material examined.—*Holotype*: U.S.A.: CALIFORNIA: *Santa Clara Co.*, 1.8 miles N of Highway 101 on Metcalf Road, 2 January 1983 (T. S. Briggs, V. F. Lee, and D. Ubick), male (CAS).

Paratypes: U.S.A.: CALIFORNIA; *Santa Clara Co.*, same data as holotype, 25 males, 20 females (CAS); 1 mile NW of Morgan Hill, 26 February 1966 (T. S. Briggs and K. Hom), male (CAS); 0.5 miles NW of Santa Teresa County Park, 27 February 1966 (T. S. Briggs), 2 females (CAS); 0.9 miles S of Junction of Silver Creek and San Felipe Roads, 27 November 1966 (T. S. Briggs and A. Jung), male, 3 females (CAS); San Jose, Silver Creek Road, 5 miles SE of Tully Road, 27 February 1966 (T. S. Briggs and K. Hom), 2 males, 12 females (CAS); San Jose, W side Silver Creek Road, 5 mi SW Tully Road, 27 November 1966 (T. S. Briggs and C. Fox), 7 males, 3 females (AMNH).

The *tiburona* species group

Diagnosis.—Members of this group have the posterior tergite margins smooth, lacking tubercles. Males differ from *homi* in having enlarged eye tubercles (Figs. 2-5) and non-telescoping styli (Figs. 8, 9, 21-33). Males may be further differentiated in having the ventral plate with only one pair of lateral setae (Figs. 21, 23, 25, 29, 31), in having a glans with apical lobes bearing a fine fringe (Figs.

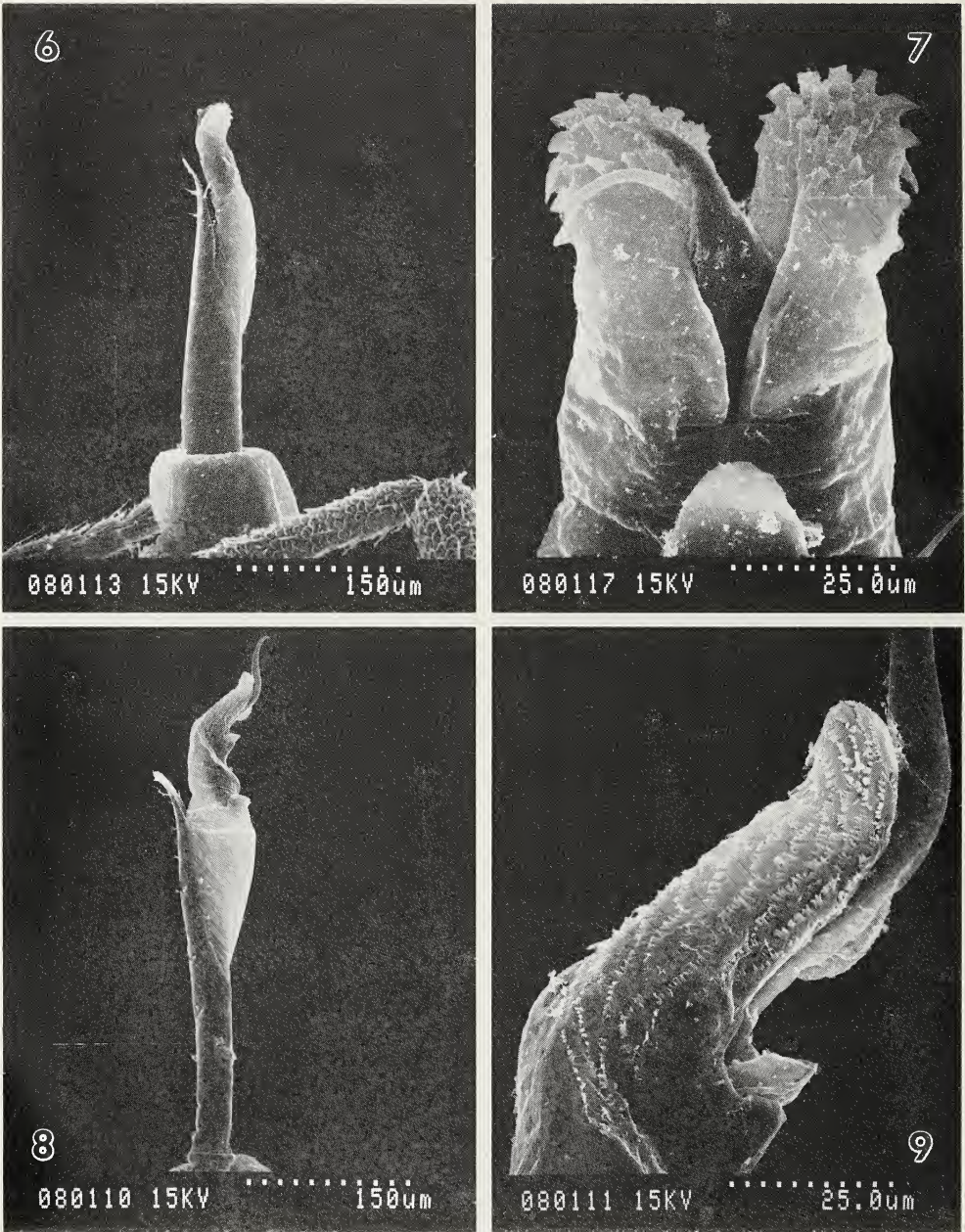


Figures 2-5.—*Microcina tiburona*, topotypes, cephalic region: 2, male, lateral view; 3, female, lateral view; 4, male, dorsal view; 5, female, lateral view. Scale bar = 0.30 mm.

22, 24, 26, 30, 32), and in having a substylar knob and a dorsal flap on the glans (Fig. 8, 9). Females have ovipositor setae with trifurcate tips (Figs. 12, 13).

Distribution.—Known only from the San Francisco Bay region (Fig. 34).

Species.—The five species representing this group can be distinguished by the male genital characters. We have not been able to discover characters for differentiating females.



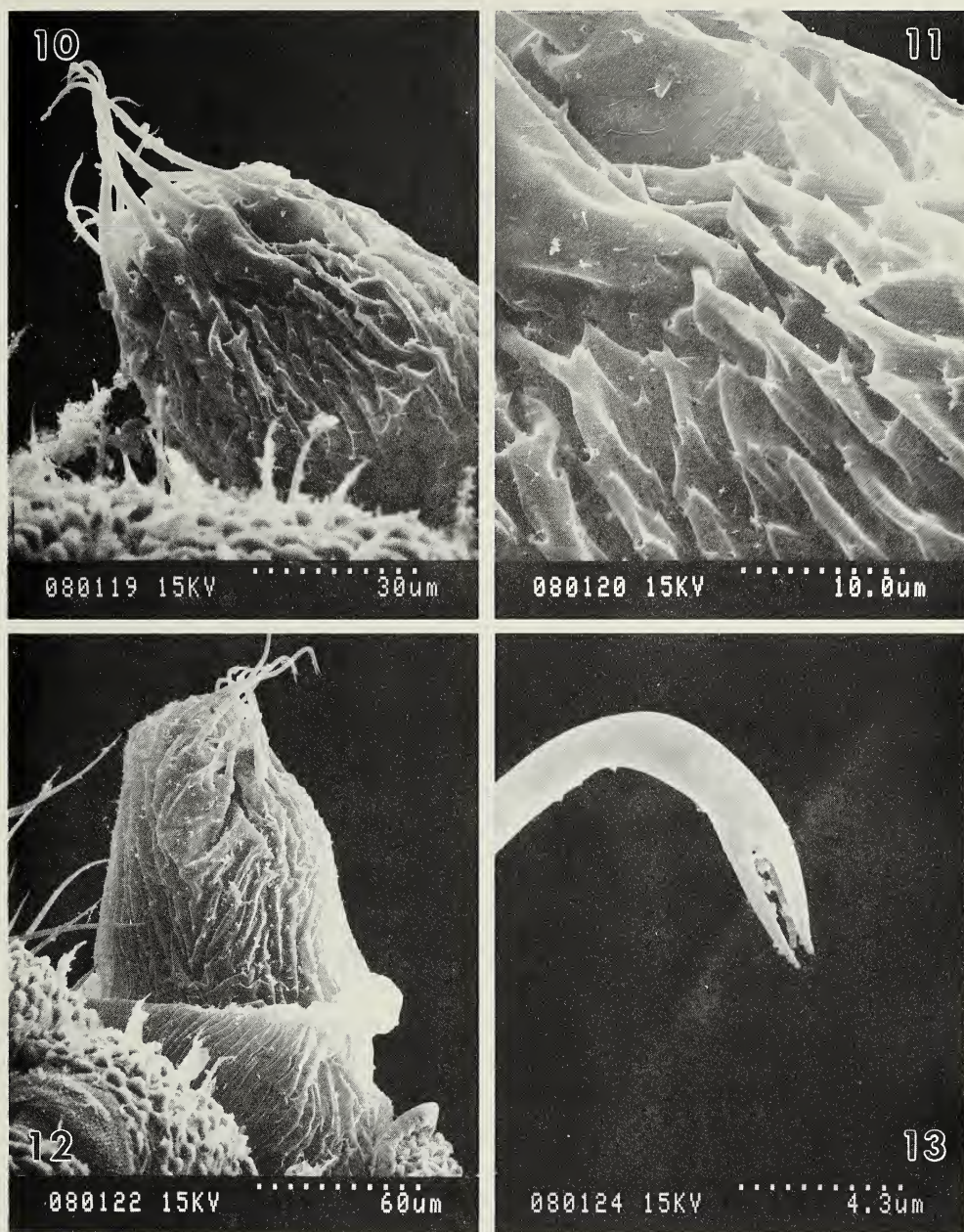
Figures 6-9.—Male genitalia of *Microcina* species, topotypes: 6, 7, *M. homi*; 6, penis, lateral view; 7, glans, ventral view; 8, 9, *M. tiburona*; 8, penis, lateral view; 9, glans, lateral view.

Microcina tiburona (Briggs and Hom), new combination

Figs. 2-5, 8, 9, 12, 13, 21, 22, 34

Sitalcina tiburona Briggs and Hom, 1966:265, Pl. 1 (figs. 2, 6). Briggs, 1968:27, (figs. 28, 58, 89).

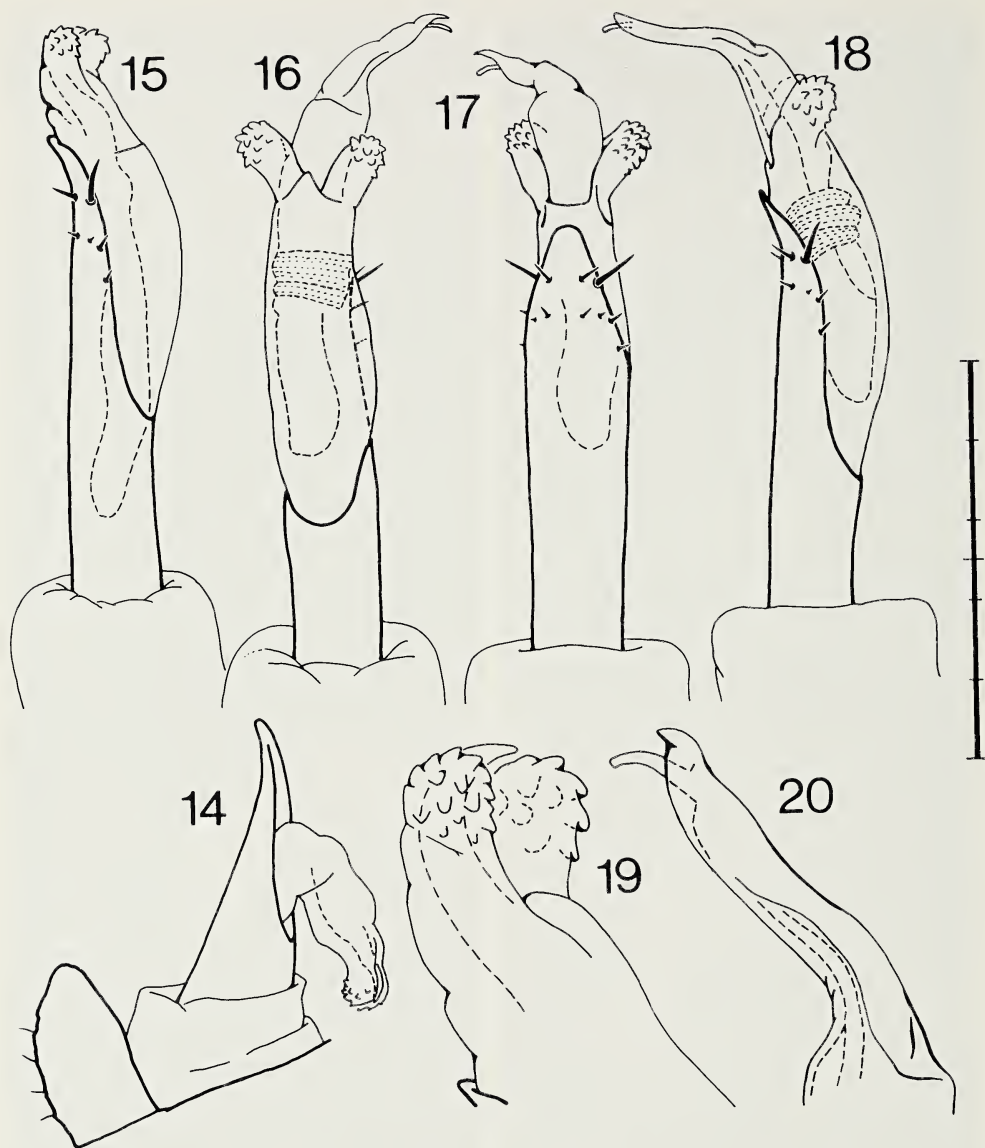
Diagnosis.—This species is distinguished from others in the group by the following combination of male genitalic characters: stylus strongly sinuous; apical



Figures 10-13.—Female genitalia of *Microcina* species, topotypes: 10, 11, *M. homi*; 10, ovipositor, lateral view; 11, ovipositor surface; 12, 13, *M. tiburona*; 12, ovipositor, lateral view; 13, ovipositor, apical seta.

lobes rounded with serrate ventral margin; and substylar knob angular (Figs. 8, 9, 21, 22).

Description.—*Male (Allotype)*: Total body length, 1.10. Scute length, 0.80; width, 0.75. Eye tubercle length, 0.24; width, 0.28. Leg II length, 1.90. Penis as illustrated (Figs. 8, 9, 21, 22).



Figures 14-20.—*Microcina homi*, male holotype (Figs. 16-18, 20), male paratopotype (Figs. 15, 19), male paratype, Silver Creek Road (Fig. 14): 14, unexpanded penis, lateral view; 15, partially expanded penis, lateral view; 16, fully expanded penis, dorsal view; 17, fully expanded penis, ventral view; 18, fully expanded penis, lateral view; 19, partially expanded glans, lateral view; 20, fully expanded stylus, lateral view. Scale = 0.25 mm (Figs. 14-18), 0.10 mm (Figs. 19, 20).

Female (Holotype): Total body length, 1.10. Scute length, 0.80; width, 0.75. Eye tubercle length, 0.20; width, 0.22. Leg II length, 2.00. Ovipositor as illustrated (Figs. 12, 13).

Natural history.—All collections are from serpentine grassland. "*Sitalcina*" *cockerelli* Goodnight and Goodnight occurs in adjacent chaparral-grassland ecotone.

Material examined.—*Holotype*: U.S.A.: CALIFORNIA; Marin Co., Tiburon, Ring Mountain, spring about 0.5 miles NE of Bel Aire School, 15 January 1966 (T. S. Briggs and K. Hom), female (CAS).

Paratypes: U.S.A.: CALIFORNIA; *Marin Co.*, same data as holotype, male (allotype), 4 males (CAS); 7 males, 3 females (AMNH), 22 January 1966 (T. S. Briggs and K. Hom), 5 males, 4 females (CAS); Tiburon, 0.5 miles S of El Campo, 22 January 1966 (K. Hom), 3 females (CAS).

Other material: U.S.A.: CALIFORNIA; *Marin Co.*, Tiburon, Ring Mountain, 19 December 1968 (T. S. Briggs), 2 males, 4 females (CAS); Tiburon, Ring Mountain, near stream between Reed Ranch Road and Ring Mountain Reserve boundary, 27 January 1985 (T. S. Briggs and K. Wang), male (CAS); 14 November 1987 (T. S. Briggs and J. Lee), 4 males, 2 females (CAS); Tiburon, end of Miraflores Lane off Avenida Miraflores, 21 December 1988 (T. S. Briggs and L. Cheng), 2 males, 2 females (CAS).

Microcina leei, new species

Figs. 23, 24, 34

Diagnosis.—This species is distinguished from others in the group by the following combination of male genital characters: stylus slightly sinuous, apical lobes pointed, and substylar knob indistinct.

Etymology.—Named after Vincent F. Lee, collector of this and many other phalangodids.

Description.—*Male (Holotype)*: Total body length, 1.10. Scute length, 0.70; width, 0.65. Eye tubercle length, 0.19; width, 0.21. Leg II length, 1.80. Penis as illustrated (Figs. 23, 24).

Female: Total body length, 0.82. Scute length, 0.63; width, 0.60. Eye tubercle length, 0.12; width, 0.17. Leg II length, 1.60. Ovipositor as in *M. tiburona*.

Natural history.—Found beneath sandstone rocks in open oak grassland where it is sympatric with *Calicina polina* (Briggs). Another phalangodid, *Sitalcina californica* (Banks), has been collected in adjacent, thickly forested areas.

Material examined.—*Holotype*: U.S.A.: CALIFORNIA; *Alameda Co.*, Berkeley, Woolsey Canyon (E of LeConte Street), N side of canyon adjacent to Lawrence Berkeley Laboratory Parking Lot, 21 December 1983 (T. S. Briggs, V. F. Lee, and D. Ubick), male (CAS).

Paratypes: U.S.A.: CALIFORNIA; *Alameda Co.*, Berkeley, N side of Woolsey Canyon, 17 February 1960 (A. Gray), male, female (AMNH); Oakland, 0.7 miles NE of Ashby on Claremont Avenue, 29 January 1983 (T. S. Briggs), male, female (CAS).

Microcina lumi, new species

Figs. 25-28, 34

Diagnosis.—This species is distinguished from others in the group by the following combination of male genital characters: stylus strongly sinuous, apical lobes rounded, and substylar knob rounded.

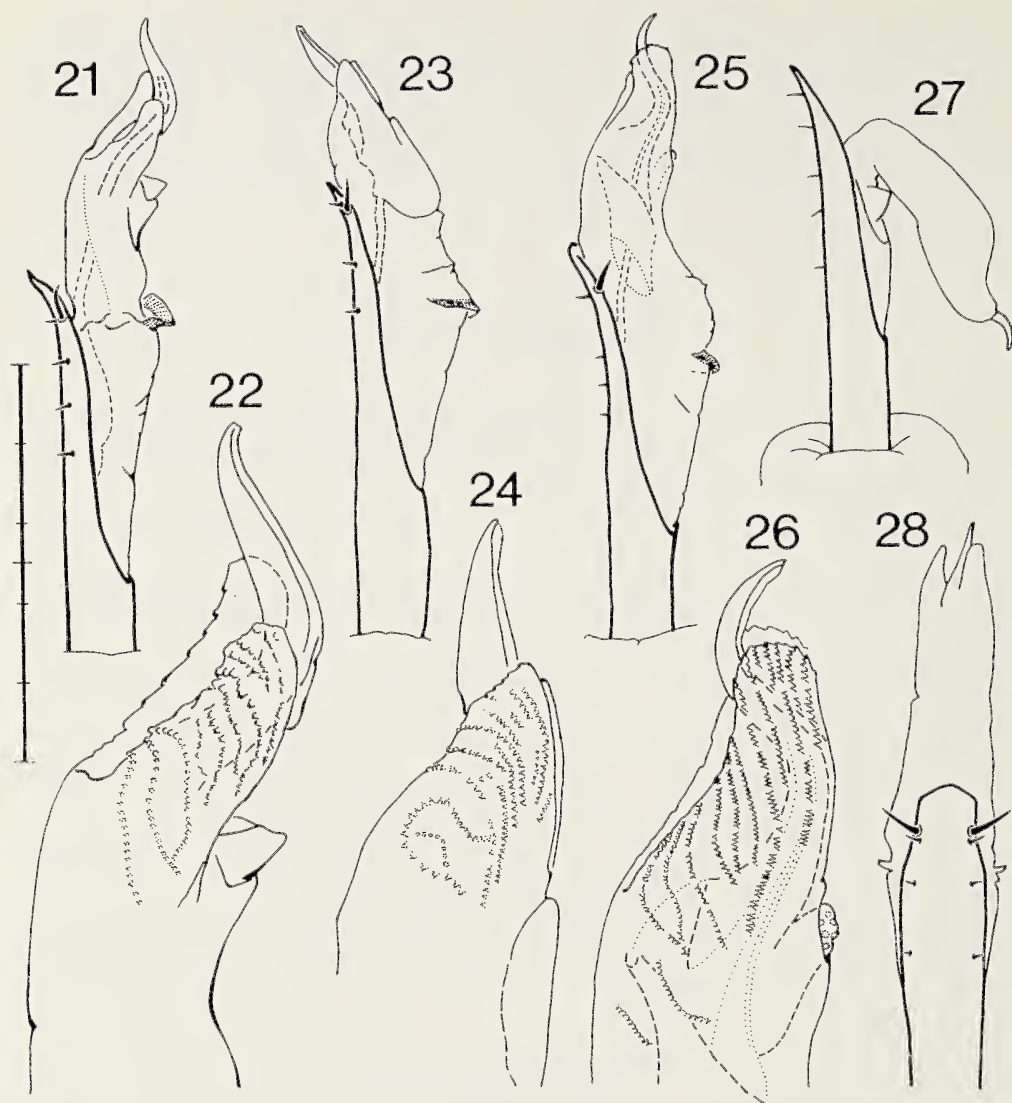
Etymology.—Named after Bill Lum, one of the collectors of this species.

Description.—*Male (Holotype)*: Total body length, 1.10. Scute length, 0.78; width, 0.68. Eye tubercle length, 0.22; width, 0.25. Leg II length, 1.80. Penis as illustrated (Figs. 25-28).

Female: Total body length, 1.00. Scute length, 0.65; width, 0.68. Eye tubercle length, 0.13; width, 0.15. Leg II length, 1.80. Ovipositor as in *M. tiburona*.

Natural history.—Found beneath serpentine rocks in grassland biomes; sympatric with *Calicina polina* (Briggs).

Material examined.—*Holotype*: U.S.A.: CALIFORNIA; *Alameda Co.*, 500 feet S of intersection of Lake Chabot Road and Fairmont Drive on W facing slope (400 feet elev.), 6 April 1982 (T. S. Briggs and D. Ubick), male (CAS).



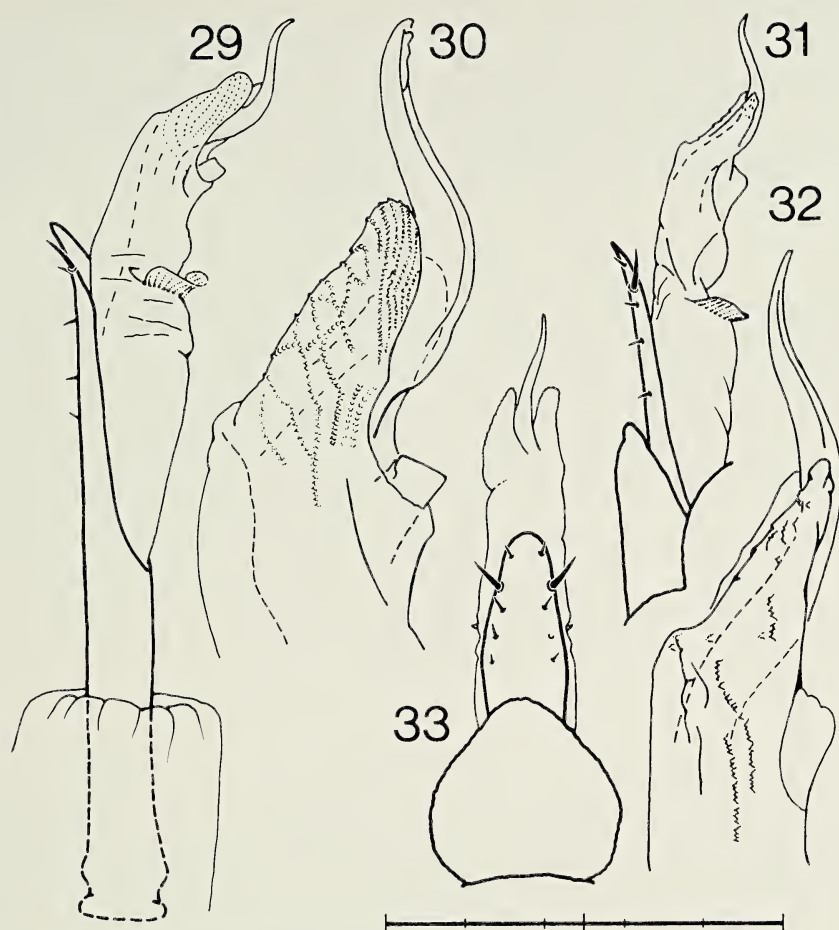
Figures 21-28.—Male genitalia of *Microcina* species: 21, 22, *M. tiburona*, topotype; 21, expanded penis, lateral view; 22, glans, lateral view; 23, 24, *M. leei*, holotype; 23, expanded penis, lateral view; 24, glans, lateral view; 25-28, *M. lumi*, holotype; 25, expanded penis, lateral view; 26, glans, lateral view; 27, unexpanded penis, lateral view; 28, expanded penis, ventral view. Scale bar = 0.25 mm (Figs. 21, 23, 25, 27, 28), 0.10 mm (Figs. 22, 24, 26).

Paratypes: U.S.A.: CALIFORNIA; *Alameda Co.*, same data as holotype, 3 females (CAS); NE San Leandro, near abandoned military road N of Fairmont Drive, 26 January 1969 (T. S. Briggs and B. Lum), 3 males, female (CAS).

***Microcina jungi*, new species**

Figs. 29, 30, 34.

Diagnosis.—This species is distinguished from others in the group by the following combination of male genital characters: stylus strongly sinuous, apical lobes rounded with smooth ventral margin, and substylar knob angular.



Figures 29-33.—Male genitalia of *Microcina* species, holotypes: 29, 30, *M. jungi*; 29, expanded penis, lateral view; 30, glans, lateral view; 31-33, *M. edgewoodensis*; 31, expanded penis, lateral view; 32, glans, lateral view; 33, expanded penis, ventral view. Scale bar = 0.25 mm (Figs. 29, 31, 33), 0.10 mm (Figs. 30, 32).

Etymology.—Named after Albert K. S. Jung, collector of this and many other phalangodids.

Description.—*Male (Holotype)*: Total body length, 1.20. Scute length, 0.88; width, 0.78. Eye tubercle length, 0.26; width, 0.31. Leg II length, 2.10. Penis as illustrated (Figs. 29, 30).

Female: Total body length, 1.10. Scute length, 0.75; width, 0.78. Eye tubercle length, 0.18; width, 0.19. Leg II length, 2.00. Ovipositor as in *M. tiburona*.

Natural history.—Found beneath serpentine rocks in grassland biomes; sympatric with *M. homi*, new species, and probably *Calicina serpentina* (Briggs and Hom).

Material examined.—*Holotype*: U.S.A.: CALIFORNIA; Santa Clara Co., 0.9 miles S of junction of Silver Creek and San Felipe Roads, 27 November 1966 (T. S. Briggs and A. K. S. Jung), male (CAS).

Paratypes: U.S.A.: CALIFORNIA; Santa Clara Co., same locality as holotype, male, 4 females (CAS).

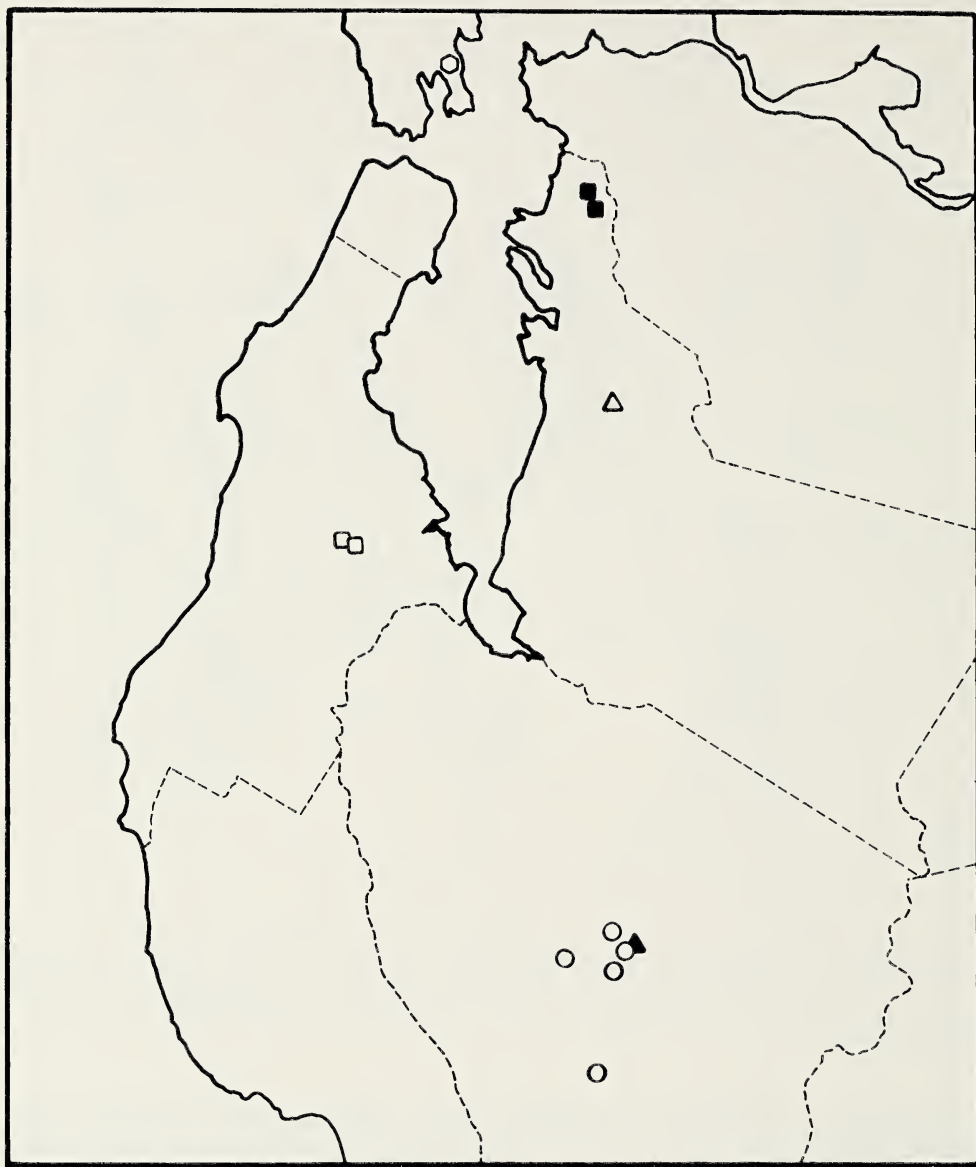


Figure 34.—Map of the San Francisco Bay Region, California, showing the distribution of *Microcina* species. *M. homi* (circles), *M. tiburona* (hexagon), *M. lumi* (open triangle), *M. jungi* (filled triangle), *M. edgewoodensis* (open squares), *M. leei* (filled squares).

Microcina edgewoodensis, new species

Figs. 31-34

Diagnosis.—This species is distinguished from others in the group by the following combination of male genital characters: stylus slightly sinuous; apical lobes strongly pointed, apically serrate; and substylar knob rounded.

Etymology.—Named after the type locality, Edgewood Park.

Description.—*Male (Holotype)*: Total body length, 0.95. Scute length, 0.68; width, 0.62. Eye tubercle length, 0.19; width, 0.22. Leg II length, 1.50. Penis as illustrated (Figs. 31-33).

Female: Unknown.

Natural history.—Found beneath serpentine rocks in grassland adjacent to scrub oaks; sympatric with *Calicina minor* (Briggs and Hom).

Material examined.—*Holotype*: U.S.A.: CALIFORNIA; *San Mateo Co.*, Edgewood Park, Canada and Edgewood Roads, 13 April 1985 (T. S. Briggs and T. Ohsumi), male (CAS).

Paratypes: U.S.A.: CALIFORNIA; *San Mateo Co.*, Edgewood Park, canyon between Sylvan and Serpentine Trails, 2 January 1987 (T. S. Briggs, V. F. Lee, and D. Ubick), 2 males (CAS).

ECOLOGY

All species of *Microcina* live in open grassland biomes and are conspicuously modified for life in xeric environments. The species are small and lightly pigmented, lack eyes, and have (relative to other phalangodids) a reduced tarsal count (3-4-4-4) and a reduced number of anterior tubercles (1 pair). Such modifications, found in only one other Nearctic phalangodid genus, *Calicina*, appear to result from two phenomena: paedomorphosis (probably progenesis) and troglobism (Ubick and Briggs 1989).

With the exception of *M. tiburona*, all species of *Microcina* have been collected with (and apparently share the habitats of) the sympatric species of *Calicina*: *M. leei* and *M. lumi* with *C. polina* (Briggs); *M. jungi* and *M. homi* with *C. serpentina* (Briggs and Hom); and *M. edgewoodensis* with *C. minor* (Briggs and Hom).

PHYLOGENY

Monophyly.—*Microcina* appears to be monophyletic on the basis of three possible synapomorphies. (1) Body cuticle sculpturing. The body cuticle of *Microcina* is areolate (Figs. 1-5), composed of an intricate honeycomb of ridges (similar to that found on the appendages of all phalangodids examined), whereas that of *Calicina* and *Sitalcina* is tuberculate. Superficial examination of the remaining phalangodids suggests that the areolate cuticle is unique to *Microcina*. Both on the basis of uniqueness and an apparently more orderly nature, the areolate cuticle appears to be derived. (2) Paedomorphic-troglobitic adaptations. The species of *Microcina* are all small and show reduction in structures (pigmentation, eyes, anterior tubercles, and tarsal count). These adaptations are absent in most phalangodids and may be synapomorphic for *Microcina*. However, the strength of this character is weakened since parallel paedomorphic-troglobitic modifications are found in species of *Calicina*. (3) Apical lobe ornamentation. The glans of *Microcina* has the apical lobes ornamented with a scale-like fringe; large in *M. homi* (Figs. 6, 7), small in the *tiburona* group (Figs. 8, 9). These structures have not been observed in species of *Calicina* or *Sitalcina*; it remains to be seen whether they are unique to *Microcina*.

Species groups.—*Microcina* contains two well defined species groups. The *tiburona* group, with five species, is characterized by a unique (at least among the North American and European phalangodids) sexual dimorphism (males have enlarged eye tubercles) and several male genitalic characters (see Diagnosis). The second group contains a single species, *M. homi*, which has an unusual glans, possibly unique, which both unfolds and telescopes during expansion.

Sister group.—The species of *Microcina* share with all other Nearctic Phalangodidae, except *Calicina*, a folding glans. Although the widespread

distribution of this state suggests plesimorphy, we have argued previously (Ubick and Briggs 1989) that the folding glans is probably derived for two reasons: (1) the folding glans is structurally more complex than the telescoping glans and (2) the folding glans is usually associated with additional and clearly derived genitalic characters, such as the bifurcate ventral plate found in *Banksula*, *Texella*, and all Appalachian genera. The folding glans is thus presumed to be a synapomorphy.

Two possible symplesiomorphies join *Microcina* and *Calicina*: (1) The telescoping glans, shared by all species of *Calicina*, also occurs in *M. homi*. In this species the glans unfolds, as in all other *Microcina*, but subsequently telescopes for complete expansion (Figs. 16-18, 20). This type of glans appears to be unique; it is not known to occur in any other species of Nearctic Phalangodidae nor in the European species examined (*Ptychosoma vitellinum* Soerensen and *Scotolemon lespesi* Lucas). (2) Both *Microcina* and *Calicina* have ovipositors bearing microspines (Figs. 10-12), which appear to be absent in *Sitalcina*. The significance of this character will be elucidated as other genera are examined. However, the character state found in *Microcina* (microspines completely cover ovipositor) appears to be plesiomorphic in *Calicina* (because of correlation with presumably plesiomorphic male genitalic characters) and may likewise be so in *Microcina*.

BIOGEOGRAPHY

Microcina is known only from the San Francisco Bay region (Fig. 34). The six species are allopatric; some are restricted to unusually small areas of suitable habitat. The single known instance of sympatry is between *M. homi* and *M. jungi*, which belong to different species groups. This suggests that the initial barrier which isolated the groups occurred in the southern part of the *Microcina* range. If dispersal did not play a significant role in the formation of the present distribution, then this barrier would have been located in what is now Santa Clara County.

ACKNOWLEDGMENTS

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**DESCRIPTIONS OF TWO NEW SPECIES OF THE GENUS
ARCHITIS (ARANEAE, PISAURIDAE) AND THE
FEMALE OF *A. VILHENA***

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ABSTRACT

Two new species of the genus *Architis* are described: *A. sinops* from a male from Brazil and *A. suarez* from a male from Colombia. The female of *A. vilhena* Carico is described for the first time.

Since the revision of *Architis* Simon (Carico 1981), a collection of specimens containing previously undescribed material has been received from the American Museum of Natural History. Herein are descriptions of two new species and of the previously unknown female of *A. vilhena* Carico extracted from this collection.

***Architis sinops*, new species**

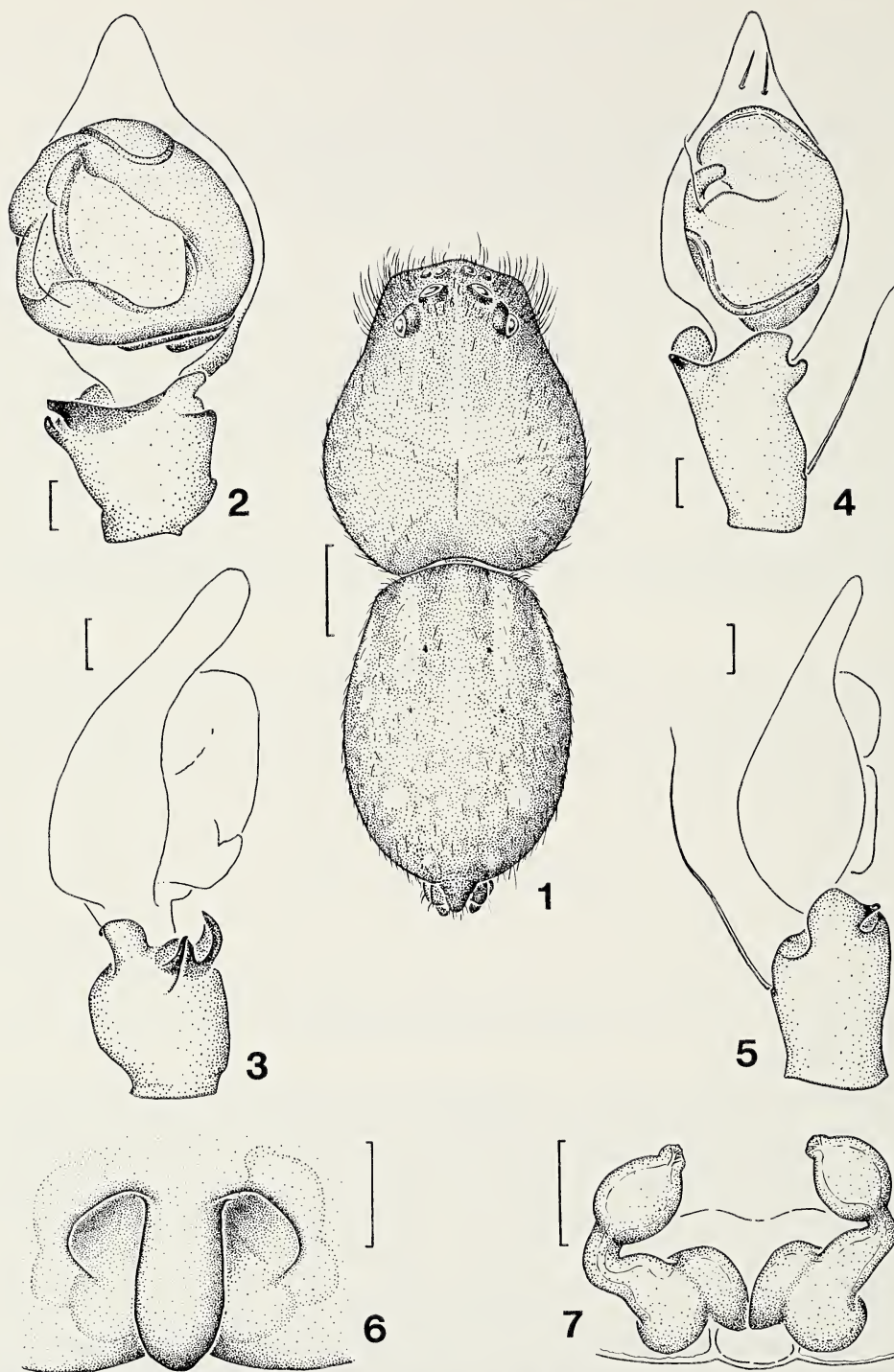
Figs. 1-3

Type.—Male holotype from Sinop, Mata Grosso, Brazil (October, 1976; M. Alvarenga), deposited in the American Museum of Natural History, New York.

Etymology.—The specific name is a noun in apposition derived from the name of the type locality.

Diagnosis.—*Architis sinops* is distinguished from all known species, except *A. capricorna* Carico, by sharing the following combination of characters: anterior eye row slightly procurved, the ALE distinctly smaller than the AME, and the clypeus height about twice the diameter of an ALE. This species is the smallest *Architis* yet discovered (total body length = 3.58 mm) which is only slightly more than half the size of its closest relative, *A. capricorna* (total body length = 6.2).

Description.—*Male holotype*: Carapace high, unmarked except for indistinct median band, each eye surrounded by distinct dark ring (Fig. 1); length 1.7, width 1.45. Sternum dusky, unmarked. Eye measurements in Table 1, anterior row slightly procurved. Leg measurements in Table 2, dusky with faint annulations. Abdomen dorsally (Fig. 1) dusky, mottled with lighter areas, cardiac area light, lighter ventrally, length 1.88. Palpus (Figs. 2, 3) with complex tibial apophysis with elements located distally on ventral, retrolateral and dorsal sides. *Female*: Unknown.



Figures 1-7.—Morphology of species of *Architis*: 1-3, *A. sinops*, male holotype; 1, dorsal pattern; 2,3, right palpus; 2, ventral view; 3, retrolateral view; 4, 5, *A. suarez*, right palpus of male holotype; 4, ventral view; 5, retrolateral view; 6, 7, *A. vilhena*, female, epigynum; 6, ventral view; 7, dorsal view. Scales: Fig. 1 = 0.5 mm; Figs. 2-7 = 0.1 mm.

Table 1.—Eye measurements of species of *Architis*. a = holotype male, b = holotype male, c = female.

Species	Diameters				Row length		Ocular quadrangle			
	ALE	AME	PLE	PME	Ant.	Post.	Ant.	Post.	Height	Clypeus
<i>A. sinops</i> ^a	0.08	0.11	0.15	0.13	0.42	0.73	0.27	0.40	0.33	0.17
<i>A. suarez</i> ^b	0.13	0.13	0.15	0.15	0.54	0.72	0.27	0.42	0.35	0.05
<i>A. vilhena</i> ^c	0.10	1.11	0.22	0.22	0.59	0.85	0.30	0.49	0.41	0.18

Natural history.—Unknown.

Distribution and material examined.—Known only from seven adult males taken in a single collection at the type locality.

Architis suarez, new species

Figs. 4, 5

Type.—Male holotype from Rio Suarez, Colombia, 1000 m, (October 1946), deposited in the American Museum of Natural History, New York.

Etymology.—The name is a noun in apposition taken from the name of the type locality.

Diagnosis.— The eyes of the procurved anterior eye row are equal in size and are only slightly smaller than eyes of the posterior row. The male of this species is further distinguished from *A. cymatilis* Carico, its sister species, by details of the palpal bulb and tibial apophysis. An additional distinction is that *A. suarez* has relatively longer legs: carapace length/leg I 0.12 compared with 0.14 in *A. cymatilis*.

Description.—*Male (Holotype):* Specimen with pattern not well preserved as a result of apparent drying out sometime after it was preserved. Carapace moderately high, each eye surrounded by a dark ring; length 1.69, width 1.50. Eye measurements in Table 1, anterior row procurved, ALE on prominent tubercles. Leg measurements in Table 2, very slender, indistinct annulations ventrally, several short stout macrosetae on ventral side of coxa and trochanter I. Abdomen somewhat shriveled, length 1.83. Palp (Figs. 4, 5) with prominent tibial apophysis projecting distally, with two distal subdivisions, ventral one acute, thickly sclerotized, dorsal one rounded, not so heavily sclerotized. *Female:* Unknown.

Natural history.— Unknown.

Distribution and material examined.—Known only from the type specimen.

Table 2.—Leg measurements in species of *Architis*. a = holotype male, b = holotype male, c = female.

Species	I	II	III	IV
<i>A. sinops</i> ^a	5.63	5.78	5.25	6.14
<i>A. suarez</i> ^b	14.56	15.12	9.66	12.44
<i>A. vilhena</i> ^c	14.0	13.9	10.6	12.2

Architis vilhena Carico

Figs. 6, 7

A. vilhena Carico, 1981:150, figs. 2, 7, 20, 21; map 2.

Female.—Color light with indistinct pattern as in male. Shape and proportions of body agrees closely with those of the male (Carico 1981). Carapace length 2.2, width 1.8. Eye measurements in Table 1. Leg measurements in Table 2. Epigynum, see Figs. 6, 7.

Note.—This is the first description of the female of this species. The collection contained 2 females and a single male from Caninde, Rio Gurupi, Para, Brazil, 7-15 April 1963, collected by B. Malkin (AMNH).

Additional new localities.—**BRAZIL:** MATO GROSSO; Barra do Taparape, 1-12 January 1963, (B. Malkin), 1 male (AMNH), Sinop, Oct. 1975, (M. Alvarenga), 5 males, (AMNH).

ACKNOWLEDGMENTS

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"EMERIT'S GLANDS" IN *CYBAEOTA* (ARANEAE, AGELENIDAE)

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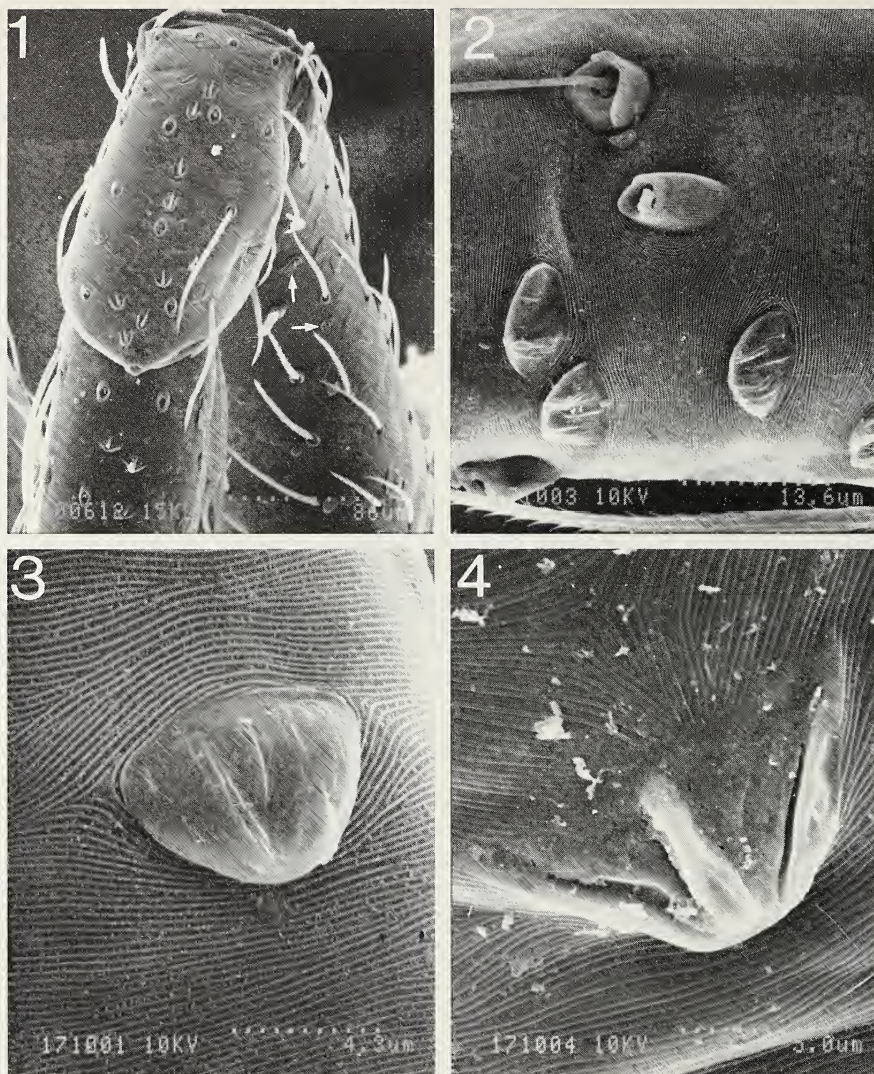
ABSTRACT

A new type of spider integumentary gland with distinctive cuticular morphology was recently described in the Telemidae. Strikingly similar glands have subsequently been found in the Leptonetidae, some Salticidae, and now in the genus *Cybaeota* (Agelenidae). The spatial distribution of the glands in *Cybaeota* is described. Their placement on the bodies of these spiders supports the repugnatorial secretion hypothesis proposed for them in the Telemidae. The phylogenetic implications of the scattered distribution of this character in spiders are discussed.

INTRODUCTION

In 1981 Emerit described a new type of integumentary structure from the legs of the cave-dwelling telemid spider *Telema tenella* Simon. In this spider he found up to twenty tiny "cupules gaufrees", or cuticular plates, randomly distributed along the middorsal length of each tibia (except on the pedipalps). Noting the presence of a minute pore in each, he suggested that the plates are either chemosensors or glands. Later Emerit and Juberthie (1983) demonstrated that the plates are glandular and produce a non-proteinaceous secretion. In two further papers (1984, 1985) Emerit described similar glands from other telemids of the genera *Apneumonella* Fage, *Usofila* Keyserling, *Seychellia* Saaristo, *Cangoderces* Harington, and *Jocquella* Baert. He concluded that the glands are most likely repugnatory in nature in spite of their lack of accumulation reservoirs normally associated with chemical defense secretions (Emerit 1984). In summary Emerit (1985) suggested that these glands are apomorphic for the family Telemidae and divide the family into two groups: *Usofila* plus *Telema* with oval plates (Figs. 2, 3), and the four others with transverse furrows.

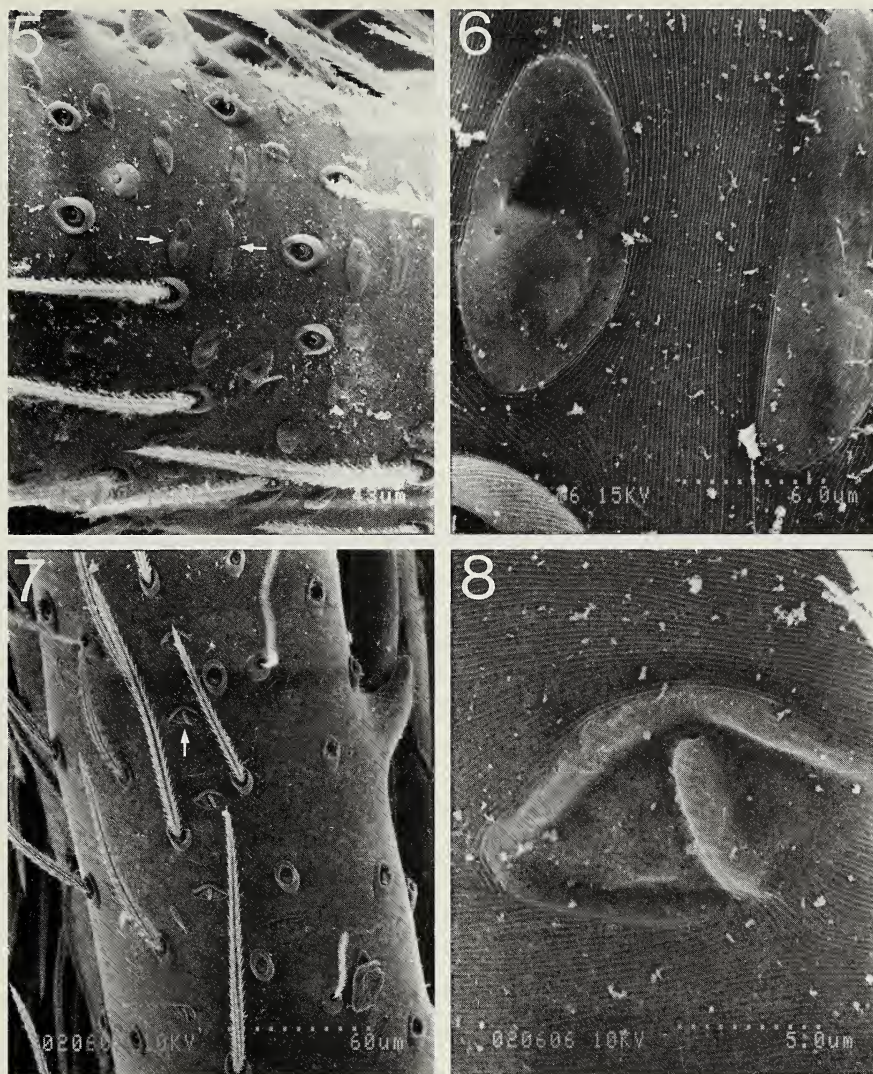
Thinking that perhaps the glands are an adaptation to troglobiosis, Emerit (1984) studied one cave-dwelling leptonetid but found no tibial glands. Platnick, however, observed glands similar to those on *Telema* and *Usofila* on the tibiae of, and Forster found them on the patellae of, some other leptonetid species (Platnick 1986). Platnick (1986) subsequently reviewed the distribution of tibial and patellar glands in the Leptonetidae and concluded that (1) a few leptonetids have oval-type tibial glands, (2) patellar glands, although lacking in the Telemidae, are found in most Leptonetidae, (3) the glands are a synapomorphy of the two families (a previously accepted but cladistically untested sister grouping), and (4) the oval morphology is probably plesiomorphic for the two families.



Figures 1-4.—Emerit's gland distribution in *Cybaeota* spp. and *Telema* sp.: 1, *C. nana*, on tibia, patella, and femur I (arrows indicate two glands on femur); 2, 3, *Telema* sp. (Victoria, British Columbia), dorsally on tibiae; 2, tibia III; 3, tibia I; 4, *C. shastae*, distodorsally on male palpal patella.

Oval glands strikingly similar to those in the telemids and leptonetids are now known to occur in at least two other families. Wanless (1984, 1987) and Wanless and Lubin (1986) have found them in the Salticidae (in a dorsal abdominal cluster in *Portia* Karsch, *Cyrba* Simon, *Cocalus* C. L. Koch, *Mintonia* Wanless, and *Gelotia syringopalpis* Wanless; dorsally on the tibiae in *Spartaeus* Thorell; and on all legs, especially femur I and patella I of males in *Diolenius minotaurus* (Wanless and Lubin). This paper describes them from the cybaeine agelenid genus *Cybaeota* Chamberlin and Ivie.

At least until their true function is determined, it is proposed here that this type of gland be termed "Emerit's glands."

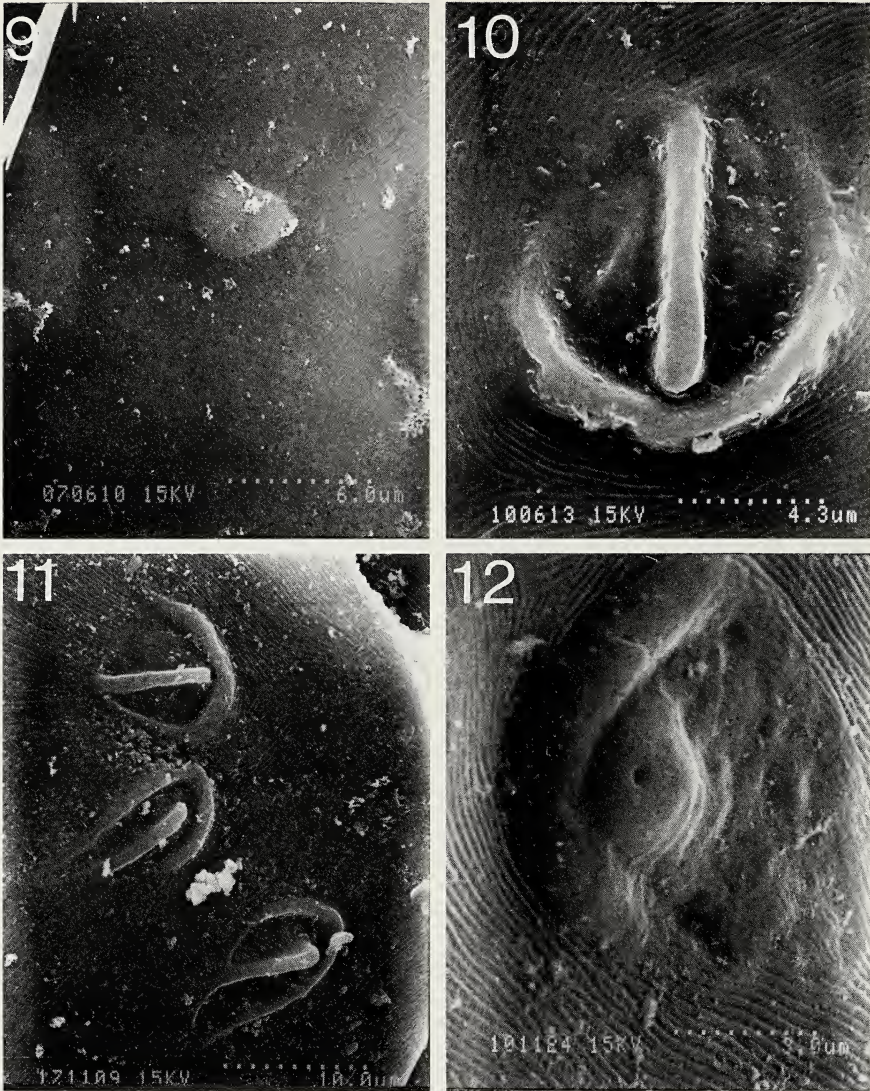


Figures 5-8.—Emerit's gland distribution in *Cybaeota* spp.: 5, 6, *C. calcarata*, proximodorsally on tibia I; 5, at least 20 glands of variable morphology; 6, two glands indicated by arrows in Fig. 5; 7, 8, *C. shastae*, mid-dorsally on tibia I; 7, five glands; 8, gland indicated by arrow in Fig. 7.

EMERIT'S GLANDS IN *CYBAEOTA* PLACEMENT, FUNCTION, AND PHYLOGENETIC IMPLICATIONS

During the preparation of a revision of *Cybaeota* (Bennett 1988) oval tibial glands were found on *C. shastae* Chamberlin and Ivie (Figs. 7, 8) which strongly resemble, in morphology and distribution, those of *Usofila*, *Telema*, and the Leptonetidae. Subsequent work with *Cybaeota* has shown that Emerit's glands occur on many parts of the body surface of *C. shastae* and at least two of the three other known species: *C. calcarata* (Emerton) and *C. nana* Chamberlin and Ivie.

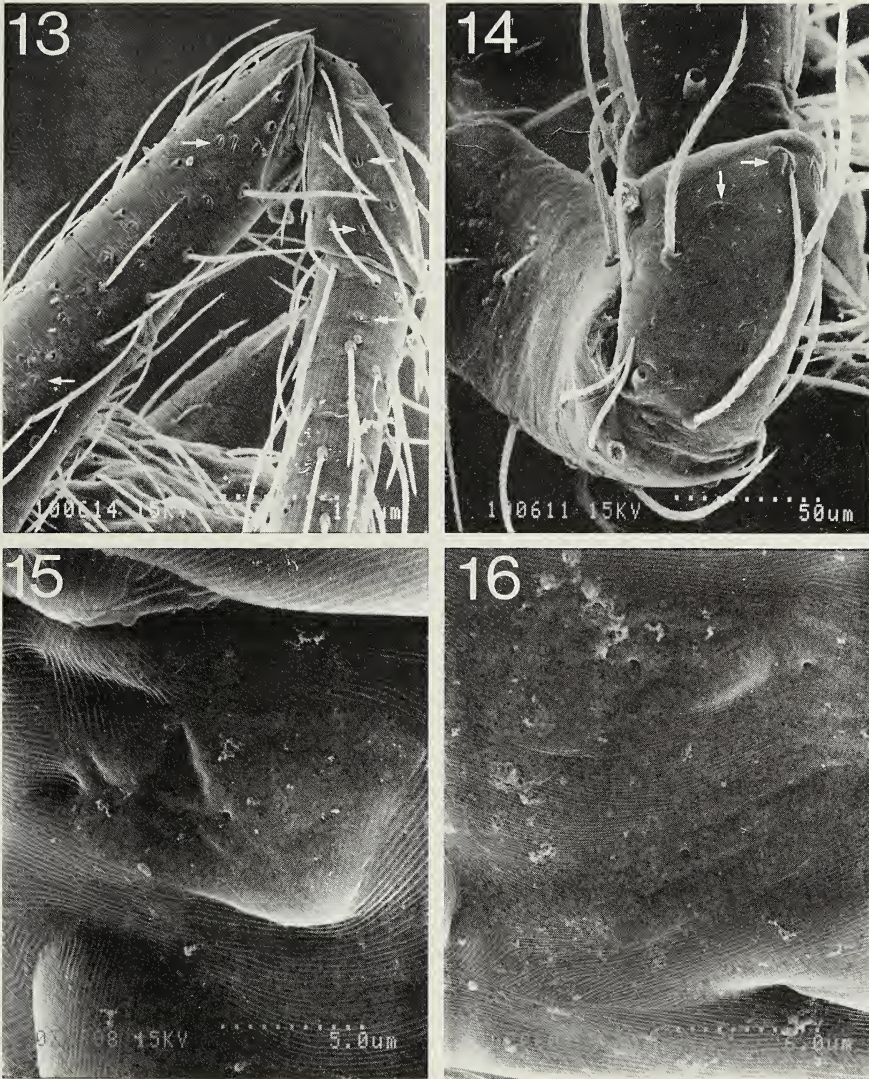
In *Cybaeota* the morphology of Emerit's glands is quite variable. There are three basic variations: distinctively keeled medially (Fig. 1), flattened with little



Figures 9-12.—Emerit's gland distribution in *Cybaeota* spp.: *C. shastae*, on anterior prolateral margin of chelicera; 10-12, distodorsally on patellae; 10, *C. nana*, patella II, female; 11, same, male; 12, *C. calcarata*, patella I.

ornamentation (Fig. 6), and laterally elongated (Fig. 25). However, intermediates and other morphotypes (e.g., Fig. 28) exist. A wide range of variation may be observed on a single specimen. This seems especially true for *C. calcarata* (Fig. 5).

All glands have a single pore which is directed distally on leg segments, anteriorly on the carapace, and posteriorly on the abdomen. The glands are most numerous and heavily concentrated on the legs - dorsally on the tibiae (Figs. 5-8) and patellae (Figs. 1, 10-12) and distolaterally on the femora (Figs. 1, 13) - and adjacent to the eye group (Figs. 17-20, 22). Glands also are encountered sporadically on the dorsal surfaces of the patellae and tibiae of palps (Figs. 4, 14-16), anteriorly on the chelicerae (Figs. 9, 21), ventrally on the coxae of legs (Figs. 25, 26), and dorsally on the abdomen (Figs. 27-29, 31, 32) or rarely ventrally (Fig.

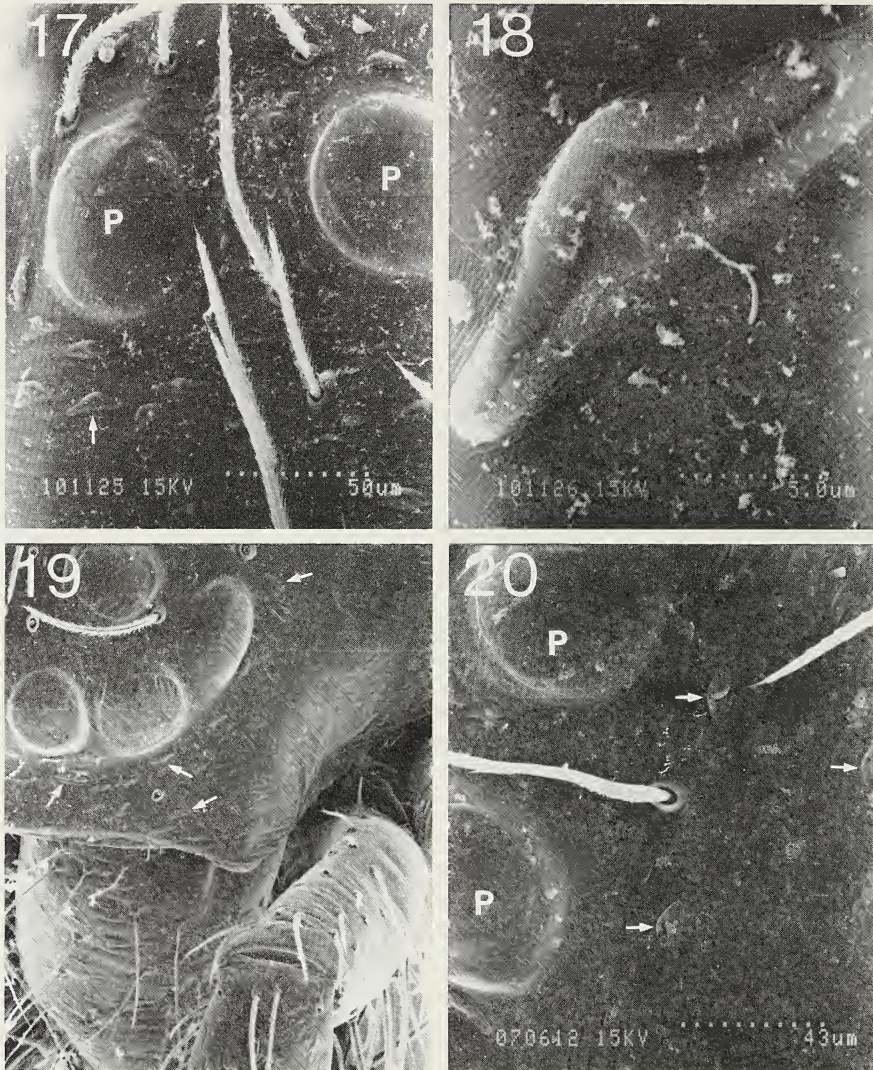


Figures 13-16.—Emerit's gland distribution in *Cybaeota* spp.: 13, *C. nana*, prolaterally on femur, patella, and tibia I (arrows indicate some of at least 20 glands present); 14-16, on female palps; 14, *C. nana*, patella (two glands indicated by arrows); 15, *C. shastae*, proximodorsal margin of tibia; 16, same, distodorsal margin.

30). Glands are also scattered about dorsally on the metatarsi of the legs (Figs. 33-36) and on the carapace (Figs. 23, 24).

In *Cybaeota*, Emerit's glands are unknown on the sternum, trochanters, tarsi, ventrally on leg segments (except the coxae), on the palpi (except as noted above), or dorsally on the femora. As in most other taxa where they are known to occur, the glands are distributed equally among males and females (see Wanless and Lubin 1986).

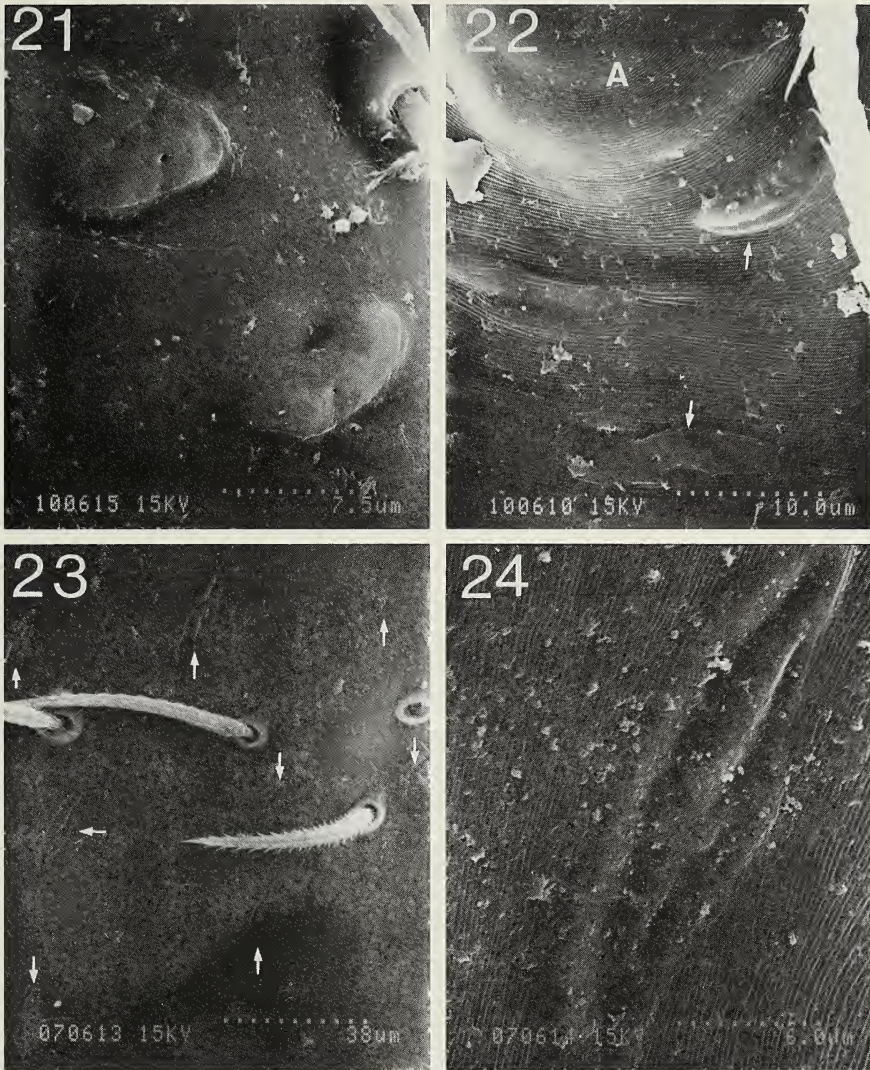
No evidence of Emerit's glands has been found in the following agelenids which exploit habitats similar to those occupied by *Cybaeota*: *Dirksia cinctipes* (Banks), *Ethobuella tuonops* Chamberlin and Ivie, *Cryphoea montana* Emerton, *Cicurina brevis* (Emerton), various species of the genera *Cybaeus* L. Koch and *Cybaeina*



Figures 17-20.—*Cybaeota* spp., Emerit's glands around eyes: 17, *C. calcarata*, posterior to PME; 18, gland indicated by arrow in 17; 19, *C. shastae*, anterior and retrolateral to left eyes; 20, same species, different specimen, posterior to PME. Arrows indicate some of glands present. P=PME.

Chamberlin and Ivie, and an unidentified species of each of *Blabomma* Chamberlin and Ivie, *Calymmaria* Chamberlin and Ivie, and one unidentified genus. Similarly, the clubionid *Phrurotimpus borealis* (Emerton), which shares conspicuous paired ventral tibial macrosetae and habitat type with *Cybaeota*, lacks this type of gland.

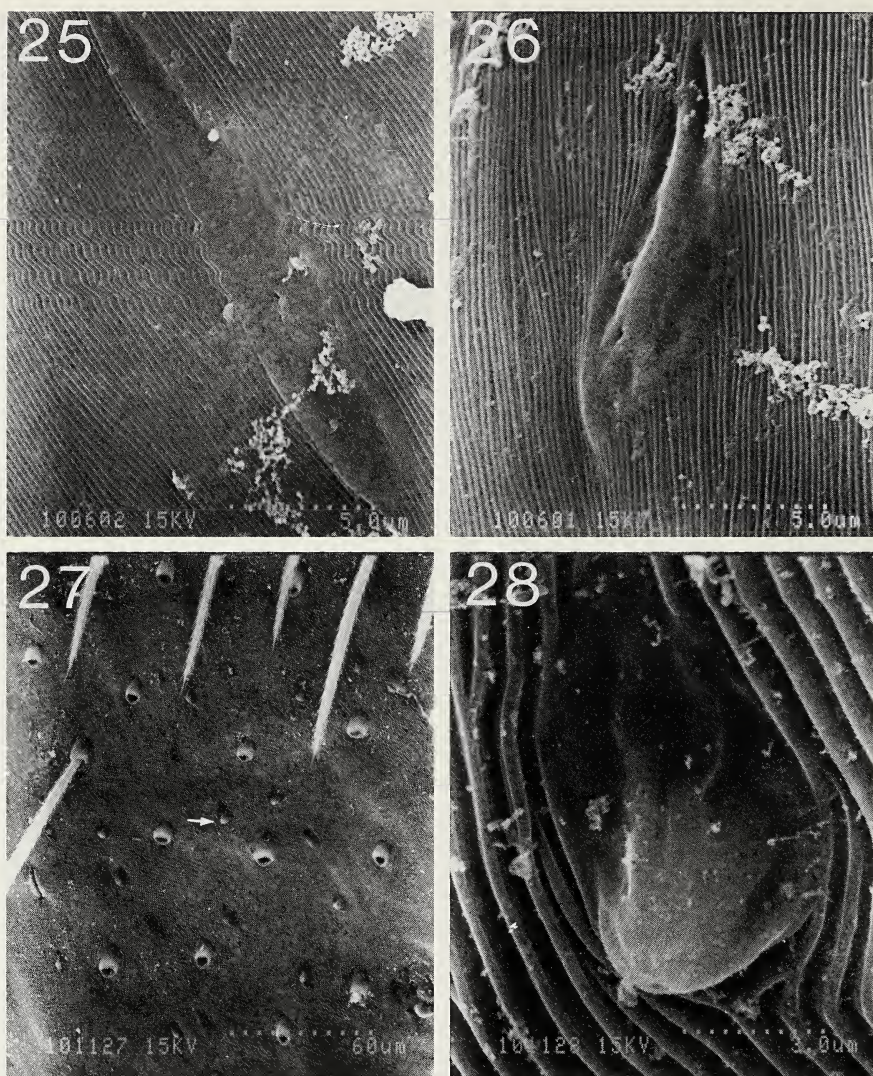
The placement of these glands on *Cybaeota* gives strong circumstantial support to Emerit's (1984) repugnatory secretion hypothesis. Like many other spiders, *Cybaeota* will often "feign death" when disturbed, folding its legs up above the carapace and bending them at the femur/patella joints. In this posture the most exposed regions of an individual are the dorsal surfaces of the tibiae and patellae and to a lesser extent the cephalic region and the ventral lateral parts of the femora. These are the same areas in which the heaviest concentrations of Emerit's



Figures 21-24.—Emerit's gland distribution in *Cybaeota* spp.: 21, 22, *C. nana*; 21, two on proximal retrolateral margin of chelicera; 22, two (indicated by arrows) below left AME; 23, 24, *C. shastae*; mid-dorsally on carapace between eye group and dorsal groove: 23, eight glands (indicated by arrows); 24, gland in Fig. 23 indicated by horizontal arrow. A=AME.

glands occur. Relatively unexposed areas (sternum, dorsal surfaces of coxae and femora, and ventral surfaces of the tibiae) or less "important" segments (tarsi) have no glands.

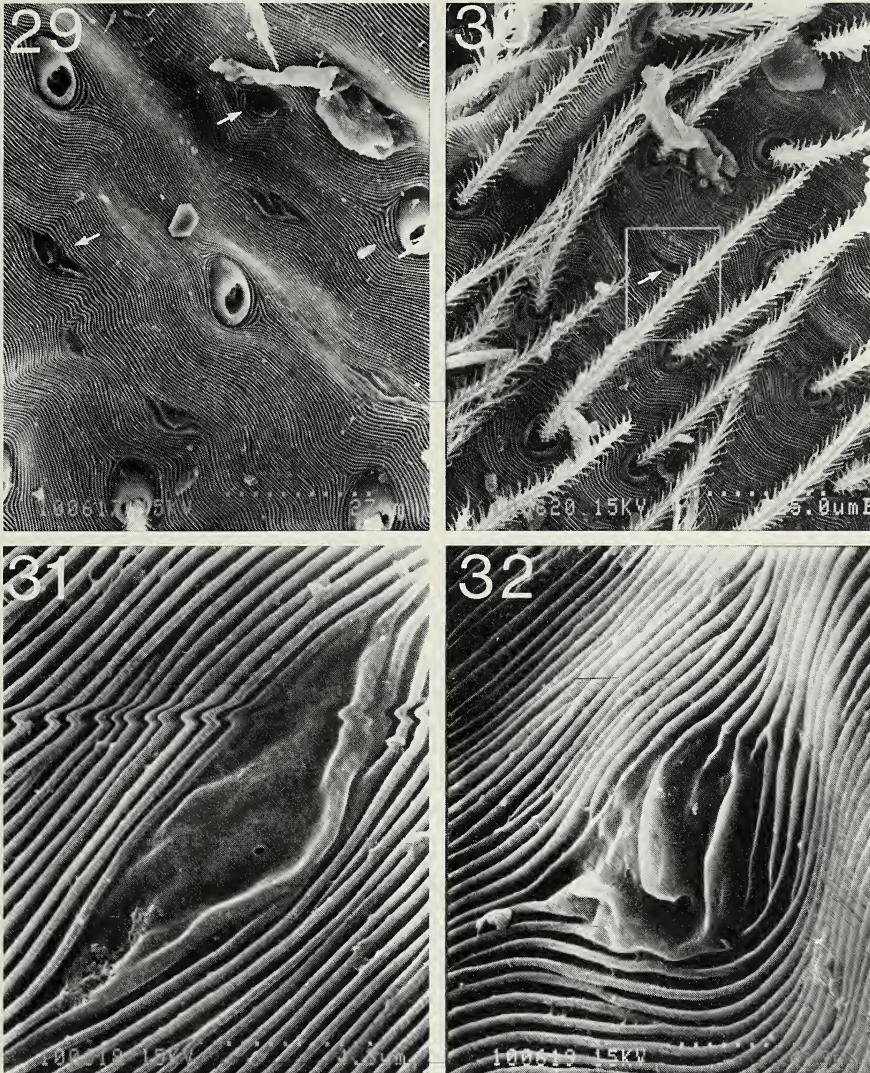
From the above overview it can be concluded that Emerit's glands appear in several distantly related groups of spiders either as a retained plesiomorphy or a frequent convergence. Because of their recently demonstrated wide distribution, it is important to reexamine the status of Emerit's glands as the sole synapomorphy of Leptonetidae plus Telemidae. Marshall (1987) has argued that in the absence of a known outgroup phylogeny the frequent occurrence of a character in the outgroup makes an equivocal polarity decision more probable and increases the likelihood that what is being interpreted as homology is actually homoplasy.



Figures 25-28.—Emerit's gland distribution in *Cybaeota* spp.: 25, 26, *C. nana*, ventrally on coxae; 25, coxa IV; 26, coxa III; 27, 28, *C. calcarata*, dorsally on abdomen; 27, at least 16 glands present; 28, gland indicated by arrow in Fig. 27.

Outgroup relationships at the family level in spiders are uncertain. It is likely that the distribution of Emerit's glands is wider than currently documented (Platnick pers. comm., Wanless pers. comm.). The probabilities of polarity error and misinterpreted homoplasy with respect to Emerit's glands are increased because of this and render this character unreliable as an indicator of monophyly. It is quite possible this character is a true synapomorphy of Leptonetidae plus Telemidae. No synapomorphies are known which contradict this grouping (Platnick 1986). For these reasons Platnick's hypothesis (1986) stands.

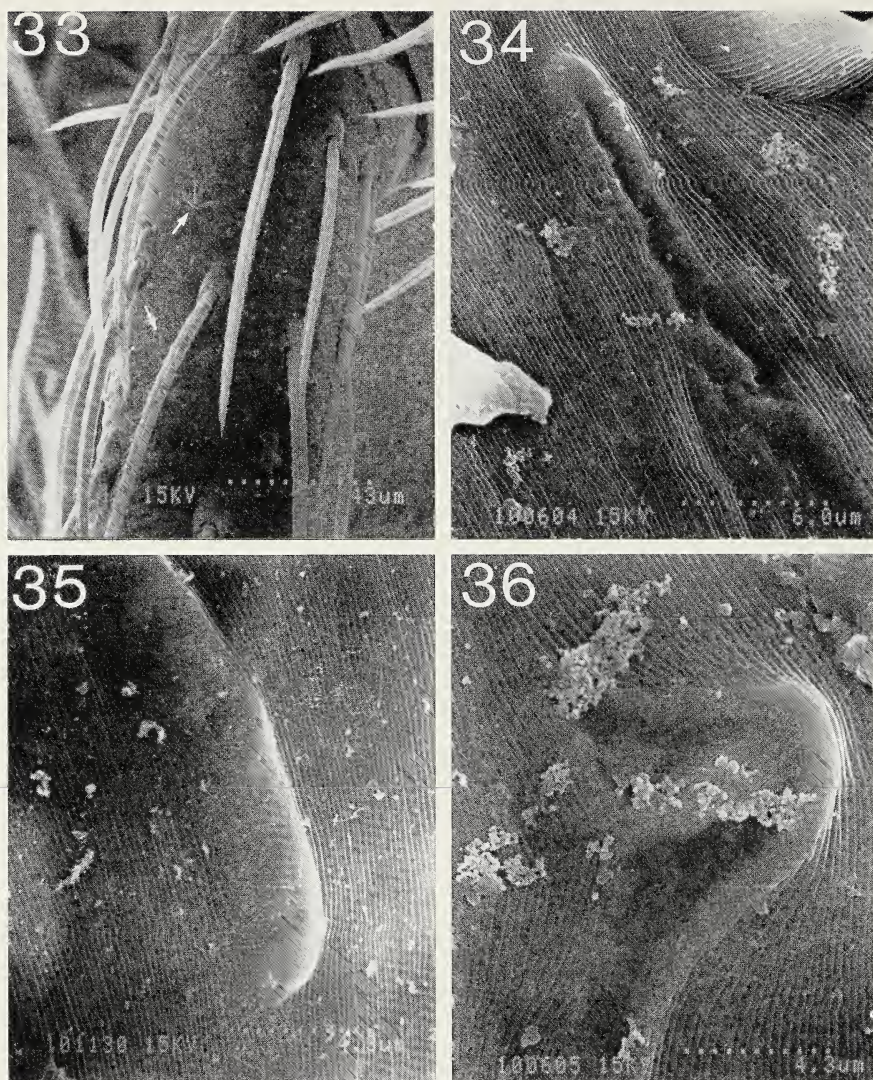
The discovery of Emerit's glands in *Cybaeota* does nothing to resolve its relationship with other spiders. *Cybaeota* remains in the Agelenidae, Cybaeinae but *incertae sedis*.



Figures 29-32.—*Cybaeota nana*, Emerit's glands on abdomen: 29, dorsal, five glands (two indicated by arrows); 30, ventral, one gland, indicated by arrow; 31, dorsal, one gland; 32, same.

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Figures 33-36.—*Cybaeota* spp., Emerit's glands proximodorsally on metatarsi: 33, *C. shastae*, two glands (indicated by arrows), leg IV; 34, *C. nana*, one gland, leg IV; 35, *C. calcarata*, one gland; 36, *C. nana*, one gland proximal to gland in Fig. 34.

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RESEARCH NOTES

SPIDER VS. SPIDER:

FRONTINELLA PYRAMITELA DETECTS *ARGYRODES*
TRIGONUM VIA CUTICULAR CHEMICALS

Interspecific chemical communication is known among spiders in the contexts of their use of chemotactile information in identifying prey species (e.g., Robinson and Olazarri 1971) and their attraction of prey species with chemical lures (Eberhard 1977, 1981; Horton 1979). We know of no reports, however, of spiders detecting and discriminating among heterospecifics that might, themselves, prey on the spiders doing the chemical sensing.

Several researchers have reported that members of the genus *Argyroides* (Theridiidae) sometimes prey upon spiders with which they cohabit in an otherwise kleptoparasitic or commensal manner (e.g., Exline and Levi 1962; Lamore 1958). Wise (1982), in an experimental field study, showed that the predatory (i.e., host-killing) behavior of *Argyroides trigonum* (Hentz) is more common than was previously realized, at least when the host is relatively small. Predation on larger spiders such as the agelenid *Agelena limbata* Thorell is also known (Tanaka 1984), and Larcher and Wise (1985) have shown that some of the relationships between *A. trigonum* and its host species can be quite complex.

One of the common hosts of *A. trigonum* in the northeastern United States is the bowl and doily spider, *Frontinella pyramitela* (Walckenaer) (Linyphiidae). The relationship between these two species is frequently kleptoparasitic but is also predatory. Archer (1946) reported *A. trigonum* preying on *F. pyramitela*, and more recently Suter (1985) reported the same phenomenon. Whatever the character of the interaction between the two species, it is certainly intense: during part of the summer, the kleptoparasite/predator inhabits about 20% of all bowl and doily webs and causes the departure or death of many of the hosts (Suter 1985). Moreover, indirect evidence suggests that the two species have interacted frequently and over a long period of time: female bowl and doily spiders, though larger than their mates, permit males to capture prey on the females' webs, and the function of that permissiveness may be to deflect (onto the males) the risk of being captured by *Argyroides* and other prey-mimicking spiders (Suter 1985).

In the work reported here, we sought to determine whether physical contact between a bowl and doily spider and its kleptoparasite/predator was chemically informative from the host's perspective, and whether the information gained was predator-specific.

Female bowl and doily spiders and the kleptoparasitic *A. trigonum* were captured on *F. pyramitela* webs in Poughkeepsie, NY, during June, 1985. Juvenile instars of a crab spider, *Misumenoides* sp. (Thomisidae) that were approximately the same size as adult *A. trigonum* were also captured in June. These eventually served as a check on whether the responses of *F. pyramitela* to contact with the

kleptoparasites' carcasses were species specific. The bowl and doily spiders were maintained in the laboratory using methods described elsewhere (Suter 1985). Soon after their capture, both *A. trigonum* and *Misumenoides* sp., as well as several *F. pyramitela*, were killed by freezing and stored frozen until they were prepared for testing.

A. trigonum carcasses were either left intact (not chemically modified) or washed in hexane for 30 minutes. Because of our experience with the cuticular pheromones of *F. pyramitela* (Suter et al. 1987), we expected that treatment with hexane would remove behaviorally active chemicals found on the surfaces of the carcasses.

The assay arena consisted of the web of an adult female bowl and doily spider with the carcass of another spider cemented to it. The carcass was cemented with droplets of Testor's paint (behaviorally neutral after drying) near the center of the underside of the bowl in the location normally occupied by the owner of the web. Several hours later, the completed arena was used in behavioral tests. At the start of a test, we released a female bowl and doily spider onto the bowl of a web that contained a heterospecific or a conspecific female carcass. Oriented search behavior (Suter 1984) usually brought the assay female into contact with the carcass after less than 30 seconds. The first contact with the carcass began the behavioral assay, which ended 5 minutes later. The initial contact and subsequent behaviors were videotaped from above while a voice record of the behaviors visible from the side of the web was made on one of the tape's audio channels. We analysed both immediate post-contact behavior and later behaviors, though we did not consider any behaviors that took place >5 minutes after initial contact.

Apart from normal locomotion, three distinct behaviors followed the assay spider's contact with a carcass: *flinch*—the rapid withdrawal of the first two pairs of legs from the immediate vicinity of the carcass without displacement of the assay spider's body; *touch-retreat*—a rapid leap away from the carcass resulting in displacement of the assay spider's body and a change in the orientation of the body relative to the carcass; and *feeding*—the insertion of the assay spider's fangs into the body of the carcass and the beginning of ingestion.

Contact with the four classes of test carcasses (intact *F. pyramitela*, intact and washed *A. trigonum*, and intact *Misumenoides* sp.) resulted in different arrays of behaviors from the assay spiders (Table 1). Contact with an intact carcass of the predatory kleptoparasite, *A. trigonum*, nearly always elicited touch-retreats from the assay spider whereas contact with *F. pyramitela* carcasses seldom did and contact with hexane-washed *A. trigonum* and with *Misumenoides* sp. never did. The assay spiders rarely fed on the carcass of an intact *A. trigonum* but often fed upon the carcasses of the other three classes of spiders.

During the five minutes of any particular test, the number of touch-retreats reflected the identity of the carcass: the host species elicited significantly fewer touch-retreats ($N = 35$, median = 0) than did the kleptoparasitic predator ($N = 71$, median = 3; 1-tailed Mann-Whitney test, $Z = -6.09$, $P < 0.001$). The orientation of the assay spider immediately after a touch-retreat also reflected, though less strongly, the identity of the carcass: following a touch-retreat, the assay spider was significantly more likely to be facing away from the carcass if the carcass was *A. trigonum* ($N = 70$, median = 120°) than if it was *F. pyramitela* ($N = 16$, median = 97° ; 1-tailed Mann-Whitney test, $Z = -1.96$, $P < 0.025$). (Note that in the

Table 1.—Incidences of behaviors performed by female *F. pyramitela* during the 5 minutes immediately following contact with the carcass of a conspecific or heterospecific spider. Decimals indicate the fraction of trials during which a particular behavior was performed.

	Incidence of			<i>N</i>
	Touch/ Retreats	Flinches	Feeding	
<i>A. trigonum</i>	0.96	0.18	0.04	28
Washed <i>A. trigonum</i>	0	0.20	0.30	20
<i>F. pyramitela</i>	0.27	0.10	0.32	30
<i>Misumenoides</i> sp.	0	0.10	0.50	20
χ^2	68.11	1.57	9.45	
<i>P</i>	<0.001	>0.50	<0.01	

preceding analysis of orientation, circular statistical tests could not legitimately be applied because the data were semicircular.) Finally, although the post-contact orientation of the assay spider and the retreat distance were positively correlated ($r = 0.373$, $P < 0.01$) over all touch-retreats, the retreat distance did not vary significantly with carcass identity.

Our results indicate that female bowl and doily spiders respond differentially to contact with the surfaces of conspecific females and two different taxa of heterospecifics. Because the major differences are eliminated after *Argyrodes trigonum* carcasses are washed in hexane, we conclude that the relevant differences are chemical rather than structural.

Because 1) the carcasses of the theridiid and the thomisid are treated very differently by *F. pyramitela* and 2) responses to carcasses of the kleptoparasitic predator are least like responses to the two other types of intact spiders, we further conclude that the assay spiders respond to the *A. trigonum* carcasses in a way that is specific to the genus or species of the carcass. The validity of this conclusion would be suspect if it were not for the apparent appropriateness of the host spider's response to contact with the kleptoparasitic predator. We know that contact with a living *A. trigonum* is sometimes fatal to the host (references above) and thus is to be avoided. We should expect, then, to find that chemotactile recognition of *A. trigonum* would be followed immediately by flight or other rapid withdrawal, and that is exactly what the data show. Because feeding requires intimate contact between the host and the carcass, we should also expect feeding on *A. trigonum* to be suppressed, and it apparently is.

The ability of bowl and doily spiders to discriminate among potential predators based on chemical information is not surprising given their similar abilities in the realm of intraspecific communication (Suter et al. 1987 and references therein). Because the detection of predators' chemicals by prey is well documented in other arthropod taxa (e.g., ants; Carlin and Johnston 1984), the near absence (Tretzel 1959) from the literature of other examples of spider-to-spider interspecific chemical communication suggests that the phenomenon demonstrated here is either rare or has been rarely sought.

The specificity and appropriateness of *F. pyramitela*'s responses to contact with *A. trigonum* carcasses suggests that the two species have interacted intensely over relatively long periods of time. The same logic suggests that one might expect to find interspecific communication of a specific and appropriate nature whenever

two spider species are known to have interacted frequently over the course of many generations. Because such relationships are probably rare, the accompanying communication may also be found only infrequently.

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AGELENA CONSOCIATA (ARANEAE, AGELENIDAE) AND ITS NEST ASSOCIATES: INSECT CLEANERS

The density of cooperative spiders within their communal nests can be high: hundreds and sometimes thousands of individuals. Refuse, such as insect carcasses and metabolic waste, present a problem to these colonies. While the cooperative spiders themselves are known to perform cleaning activities (pers.

obs.), other arthropods associated with the nests, in particular lepidopteran larvae, have been reported to play a role in refuse removal (Pocock 1909; Robinson 1977). Pocock (1909) observed small larvae of the moth, *Batrachedra stegodyphobius* Walsingham, eating insect carcasses in the nest of an unidentified species of social eresid, *Stegodyphus* sp. in South Africa. Robinson (1977) studied this cleaning behavior under laboratory conditions in another moth larva, *Neopalthis madates* Druce, that is found in the nests of the new world social theridiid, *Anelosimus eximius* (Keyserling).

We report here on our field observations of arthropod nest associates of the West African social spider, *Agelena consociata* Denis. Five nests of this species located on the M'Passa Reserve of The Institut de Recherche en Ecologie Tropicale, near Makokou, Gabon, were intensively studied during the period from October 16 to December 5, 1987. Forty-eight hours during this period, made up of 30-minute segments, was devoted to direct observation on the nests for prey encounters. The presence and activity of insects in the nest area as well as the spiders' reactions to this activity, was recorded for each encounter. Each nest was rotated through a schedule such that all nests were observed for equal amounts of time at the same set times each day. Field identifications only were made of most of these taxa because we wished to avoid disruption of colony activities. We were able to collect ants without disruption because of their numbers. These were identified to genus.

A total of 791 individual insects were seen in the nests of *A. consociata* during the course of these observations. Fifty-two of these insects were attacked and eaten. Others escaped or were repelled. Three types of insect were tolerated, lepidopteran larvae, tenebrionid beetles and some small ant species.

Lepidopteran larvae were only observed in the largest, and presumably oldest, nest under observation. Brach (1977) noted that the older nests of *Anelosimus studiosus* (Hentz) were more likely to contain inhabitant arthropods. Brach observed these larvae to move in rapid and seemingly random spaced jerks with long intervals of motionlessness. Catepillars in the *Agelena* nest were never seen to move across the surface of the webbing but remained in the leaf and web tangle that made up the central retreat, where there tends to be a build-up of detritus. There were no observations of spiders approaching these larvae or even orienting toward them.

In addition to the lepidopterans that may be common to social spider nests, beetles were frequently seen in all nests regardless of nest size and presumed age. At least three species of tenebrionids were observed to have free access to most areas of the colony, walking across the surface of the sheet or inside the nest retreats. These beetles were occasionally touched by spiders but for the most part were otherwise ignored. Twice an attack occurred when a tenebrionid beetle came very close to a cluster of egg sacs. The beetles were driven away by groups of mature female spiders, that tended to be found hanging from the underside of these eggs. In these cases the beetles were not killed but merely expelled from the immediate proximity of the eggs. *Agelena consociata* discriminated this beetle type from others such that upon contact, varying forms were eaten or carried to the edge of the sheet and dropped over the side.

All of the nests under regular observation housed ants which were seen to be active in all but one nest in at least 20% of the observation periods. The ants, of the genera *Pheidole* and *Technomyrmex*, were approached by the spiders as they

walked across the surface of the webbing. They were also sometimes touched by *Agelena* but were never attacked. Other ants discovered by the spiders on the sheet, even much larger species, were attacked.

A simple experiment, completed at six nests other than those under daily observation, demonstrated the nest cleaning activity of these ants. Plastic petri dishes enclosing freshly killed (by freezing) moths were placed on the webbing of each nest. The lids were closed such that *Agelena* could not enter them. After 6 hours the nests were revisited. All dishes were found to contain ants and in two of the cases the carcasses had already been completely consumed.

In summary, lepidopteran larvae inhabiting the webs of social spiders in the families Theridiidae and Eresidae have been reported. To our knowledge this is the first account of a similar system in the social agelenids. The lepidopteran larvae reported for other social spiders were less prominent than ants and beetles in this system. Although we have documented cleaning activity only for the ants, observations by others suggest that the larvae at least function in this capacity as well.

We thank Marcel Bilombi for help in locating *Agelena* nests and Carole Capel whose assistance in data collection was invaluable. We also wish to thank Dr. M. Lacey at the systematic entomology laboratory at the USDA who identified the ants for us. This report was supported by a National Science Foundation grant (BSR-8314900) to S. E. Riechert.

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SUBMERSION SURVIVAL IN AERIAL WEB-WEAVING SPIDERS FROM A TROPICAL WET FOREST

INTRODUCTION AND METHODS

Previously I found that several species of temperate zone, web-weaving spiders that dwell beneath stones possess morphological and behavioral adaptations that enhance underwater survival (Rovner 1986). These spiders retain large air stores on the body surface in their dense setal coats; furthermore, they usually show minimal or no locomotor activity when submerged. Both factors adapt them for

surviving rain-caused flooding. On the other hand, the aerial web-weavers I tested—*Achaearanea tepidariorum* (C. L. Koch), *Araneus marmoreus* Clerck, *Micrathena gracilis* (Walckenaer), and *Prolinyphia marginata* (C. L. Koch)—were less able to resist drowning. This may have resulted from the fact that their setal coats retained either a small ventral air store or none at all. Also, the araneids showed intense locomotor activity at the beginning of the test, which was followed by immotility very early in the test period. After removal from the water, these four species either became active only after a relatively long time or not at all, i.e., they had drowned. The high metabolic rate of araneids (Anderson 1970) may have played a role in their drowning so quickly. However, the relative size of the air store on the body surface and the level of activity were the only factors I examined.

I subsequently hypothesized that these two factors that conferred drowning resistance are sufficiently plastic within spider families as to be significantly modified by selection imposed by local conditions. I anticipated that aerial web-weaving spiders from a life zone typified by frequent, heavy rainfall (with possible local flooding) would possess greater drowning resistance than temperate deciduous forest species.

Here I tested seven species from a lowland tropical wet forest site; six were araneids and one a theridiid. Work was conducted during a 6-week stay at the Organization for Tropical Studies' La Selva station near Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica (mid-November to late December, 1987). Female spiders were collected near trails in the forest—*Micrathena brevipes* (O. P. Cambridge), *Micrathena molesta* Chickering, *Micrathena schreibersi* (Perty), *Nephila clavipes* (Linn.), and *Achaearanea toeniata* (Keyserling); in the clearing surrounding the station buildings—*Argiope savignyi* Levi and *N. clavipes*; and on a footbridge over the river—*Metazygia* sp. Voucher specimens are deposited in Harvard University's Museum of Comparative Zoology.

Within a few days of capture, 10 individuals of each species were submersed one at a time for 1 h in 25°C distilled water, aerated prior to use. This occurred in a completely filled, covered, all-glass miniature aquarium of an appropriate size (27 or 70 ml) for the species being tested. (The inside bottom and back wall had a white paper liner that provided a surface to which the spider could cling). Adult *N. clavipes* were tested in a 260-ml paper cup with a plastic lid.

Each spider was anesthetized with CO₂ to facilitate placement in the water; timing began when the spider resumed movement. As pointed out by J. F. Anderson (pers. comm.) the use of CO₂ for anesthesia complicates the analysis since the gas affects respiratory processes. However, CO₂ anesthesia was the only means available to me to achieve a uniform initiation of each test. Grasping an unanesthetized spider to hold it beneath the water during placement of the lid on the aquarium could have caused overexcitement or even injury in some spiders. (An aquarium with a bottom inlet and top outlet to allow filling after placement of the spider and lid closure would prevent the need for anesthesia in future studies.)

I also wished to conduct some preliminary observations on species differences in reaction to contact with water and in buoyancy. For this purpose, several individuals of each species were placed on the surface of water contained in a plastic basin. After observing the nature of possible behaviors that would improve

Table 1.—Activity, typical behaviors, and mortality of spiders subjected to a 1-h submersion (25°C), listed in rough order of increasing likelihood of drowning after submersion. Percent of h spent in locomotion is given as $\bar{x} \pm SD$ (range); N = 10.

Species	Percent locomotion	Typical behaviors	Deaths
<i>Micrathena molesta</i>	3.6 \pm 2.7 (0.8 – 7.8)	rapid crawl/inactive; mobile < 15 min	2/10
<i>Metazygia</i> sp.	6.1 \pm 4.1 (0.1 – 13.2)	rapid crawl/inactive; mobile < 25 min	6/10
<i>Achaearanea taeniata</i>	3.6 \pm 2.2 (1.4 – 8.8)	rapid crawl/inactive; mobile < 15	7/10
<i>Micrathena brevipes</i>	3.1 \pm 0.8 (2.2 – 4.5)	thrash on bottom; mobile < 10	7/10
<i>Micrathena schreibersi</i>	2.7 \pm 0.8 (1.5 – 4.0)	thrash on bottom; mobile – 10	7/10
<i>Argiope savignyi</i>	2.2 \pm 1.1 (0.6 – 4.0)	slow or rapid crawl; mobile < 10 min	7/10
<i>Nephila clavipes</i> juv.	2.3 \pm 1.9 (0.1 – 5.4)	slow crawl or thrash; mobile < 10 min	9/10
<i>Nephila clavipes</i> adult	0.9 \pm 0.9 (0.1 – 2.4)	slow crawl or thrash; mobile < 5 min	9/10

survival, I gently pushed each spider beneath the surface to see if it showed buoyancy after losing contact with the surface film.

RESULTS AND DISCUSSION

In six of the seven species, more than half of the individuals drowned as a result of the 1-h submersion (Table 1). Such high mortality levels had occurred in only one of the four temperate zone aerial web-weavers (*Micrathena gracilis*) that I tested previously. On this basis, it is evident that the aerial web weavers that I tested from the tropical wet forest are not any better adapted for drowning resistance than are those tested from the temperate deciduous forest biome.

During submersion, most of the wet forest species were motile for less than 15 min (Table 1), a level of endurance similar to that shown by the two temperate zone araneids tested previously. *Metazygia* sp., which had built webs on a footbridge above the river, was able to remain motile the longest and, of all the species tested here, spent the greatest percentage of the hour in locomotion. *Micrathena molesta* was the most resistant of the spiders to drowning during submersion; however, there was no obvious factor to account for its superior endurance. Least resistant to drowning were adult *Nephila clavipes*, which became immotile after a very brief initial period of slow crawling or very slow thrashing. If submerged during rain-caused flooding in the field, adults of this species would survive only briefly while attempting to climb above the water's surface. Juvenile *N. clavipes* showed longer periods of motility but nonetheless drowned as often as the adults in the 1-h test (Table 1). The remaining araneids—*M. brevipes*, *M. schreibersi*, and *A. savignyi*—fared little better than *N. clavipes*. The single theridiid tested, *A. taeniata*, was similar to the best-adapted araneid, *M. molesta*, as to percent locomotion and duration of motility but drowned as frequently as the last-mentioned group of araneid species.

I also studied the effects of placing individuals of the seven species on the surface of an open pool of water in a basin. Pushing each floating spider beneath

the surface revealed a difference in buoyancy between two groups of species. The three *Micrathena* species, *Metazygia* sp., and *N. clavipes* sank to the bottom, whereas *Argiope savignyi* and *Achaearanea taeniata* usually were buoyed up, apparently by having a temporary air store on the body surface of relatively large size for the mass of the spider. The gas store in the booklungs and the hydrophobic nature of the cuticle also may have influenced buoyancy (J. F. Anderson pers. comm.).

Of additional interest were differences among the species' responses to contact with the water's surface film. Three species—*A. taeniata*, *Metazygia* sp., and *N. clavipes*—floated on their sides with their legs drawn in, a behavior that kept one or both lung slits exposed to the air. The three *Micrathena* species and *A. savignyi* usually floated upright, with their lung slits below the surface. Although *A. savignyi* had an opisthosomal air film that probably maintained an air supply channel from its slits to the air above the water, that did not seem to be the case for the three *Micrathena* species, which have relatively few opisthosomal setae. However, one of these, *M. brevipes*, showed a behavior that solved the dilemma. By lifting its massive opisthosoma to a position above the carapace, the spider then further rolled into a partial "flip" and ended up in an inverted position. Thus, now floating on its dorsal surface, the spider avoided drowning.

The data presented here and in my previous study (Rovner 1986) suggest that araneids—even those of tropical wet forests—can withstand only relatively brief periods of submersion, compared to web-weavers that dwell beneath stones. Apparently, the features that provide drowning resistance in spiders are general to the families possessing them and cannot be readily modified to adapt species of other families to local conditions. Indeed, the marsh-dwelling araneid *Acanthepeira venusta* (Banks) in Florida, which climbs down into the water when disturbed, has relatively brief submersion periods of 3 min or less (Folkerts and Mullen 1987). On the other hand, the absence of adaptations for aquatic conditions in aerial web weavers of the tropical wet forest may suggest that these spiders are usually able to avoid falling into floodwaters during heavy rain and that, if they do fall onto the water, they may have adaptations reducing the possibility of submersion or drowning after being trapped in the surface film.

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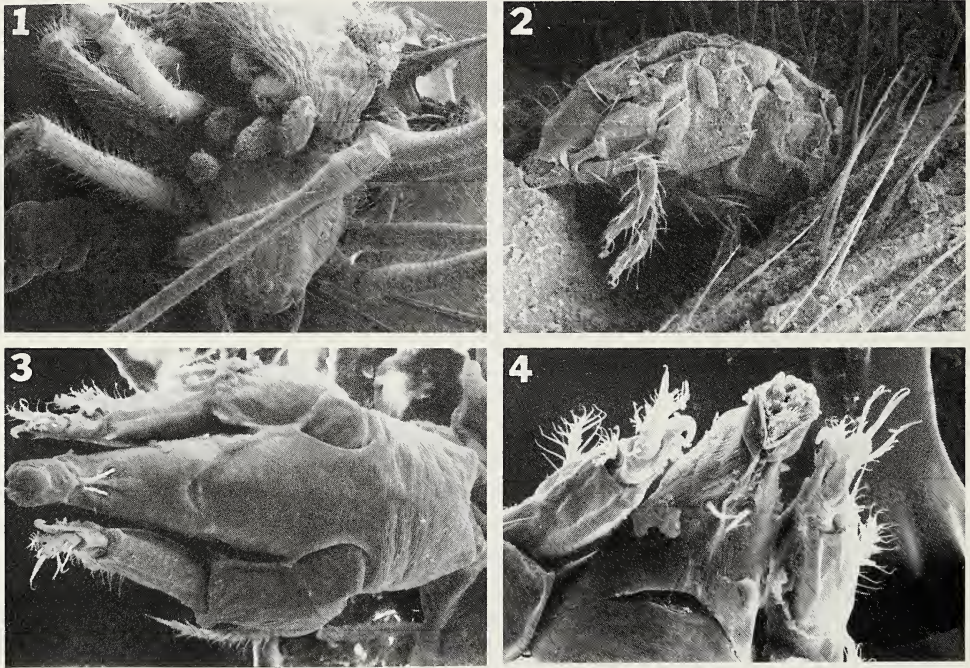
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**MITE PARASITISM OF THE POLYMORPHIC SPIDER,
ENOPLOGNATHA OVATA (ARANEAE, THERIDIIDAE),
FROM COASTAL MAINE**

INTRODUCTION AND METHODS

The theridiid spider *Enoplognatha ovata* (Clerck) is a common inhabitant of weedy vegetation along the northeastern seaboard of North America. Recent research into the ecological genetics of color polymorphism in *E. ovata* in Maine populations (Reillo and Wise 1988a, b, c) has uncovered considerable parasitism of this species by larval Parasitengona mites. Here I present parasitism frequencies for color morphs of mature female spiders from 15 natural populations.

Thirty-five coastal Maine populations of *E. ovata* were censused during mid-August from 1986-1987. Populations were distributed between Boothbay, ME (43°50' N. Lat./69°37' W. Long.) and Acadia National Park at Mt. Desert Island (44°25' N. Lat./68°15' W. Long.) (see map in Reillo and Wise [1988b]). Descriptions of the color phenotypes and life history of *E. ovata* can be found elsewhere (Seligy 1971; Oxford 1976; Wise and Reillo 1985), and censusing techniques for estimating morph frequencies are discussed in Oxford (1976, 1985a, b) and Reillo and Wise (1988b). Spiders were examined for mites in the



Figures 1-4.—Scanning electron micrographs of *E. ovata* host and Parasitengona mites: 1, adult female spider with trombidid mites clustered on opisthosoma (32X magnification); 2, trombidid mite with gnathosoma attached to host at left (260X); 3, gnathosoma of erythraeid mite, dorsal view (940X); 4, gnathosoma, ventral view, showing subcapitulum and palps (1500X).

field with the naked eye. Samples of hosts and mites were preserved in alcohol or by freezing. Specimens were identified by W. Calvin Welbourn, curator at the acarology laboratory of Ohio State University.

RESULTS AND DISCUSSION

Two families of mites were found among the samples: Trombidiidae, likely *Trombidium auroraense* or a close relative (Figs. 1, 2); and Erythraeidae, probably of the genus *Leptus* (Figs. 3, 4). Mites were encountered only as larvae (six legs), bright orange in color, usually attached to the host on the dorsal side along the margins of the carapace or on top the opisthosoma, with clusters often nestled on or adjacent to the pedicel (Fig. 1). Total body length ranged from 0.20 mm to >1.0 mm and varied with the extent of engorgement. The number of mites per host was not scored in the field, but examination of preserved specimens usually revealed one or several larvae/host, with occasional heavy loadings in excess of 15 larvae/host.

Since not all mites scored in the field were collected and identified, I will present gross parasitism frequencies for both mite families collectively. Mites were found among 15 of the 35 censused populations (Table 1). The frequency of parasitism among mature females was highly variable for affected populations, ranging from 0.1% to 20.7% (mean \pm SE for all populations and years = 0.057 ± 0.012). Mites were also observed among immature spiders of both sexes and mature males, but small sample sizes for these categories prohibited estimating parasitism frequencies. No clear association between mite incidence and environment could be detected; however, populations inhabiting edge vegetation along open fields or areas beneath sparse canopy appeared to consistently contain mites whereas shaded populations were generally found to be mite-free.

Parasitism frequencies did not change significantly between 1986 and 1987 for three of five populations having frequencies $\geq 3\%$ for both years (populations BPP, NL1, MP; Table 1; Chi-squares ≤ 1.46 , $df = 1$, continuity correction, $P \geq 0.226$). For the other two populations, parasitism in one (population DM) more than doubled (Chi-square = 6.74, $df = 1$, continuity correction, $P = 0.009$), while in the other (population NL2) it decreased by nearly half (Chi-square = 7.73, $df = 1$, continuity correction, $P = 0.005$).

I found no evidence of differential parasitism of color morphs of the host *E. ovata*. For populations in which phenotype and parasitism frequencies were sufficient to conduct contingency chi-square tests (populations MP, NL1, NL2, DM; Table 1), parasitism was random with respect to phenotype in 1986 (Chi-squares ≤ 4.07 , $df = 2$, $P \geq 0.131$) and 1987 (Chi-squares ≤ 4.66 , $df = 2$, $P \geq 0.097$). I also found no evidence that parasitized females reproduced less successfully than non-parasitized females. For populations with total number of parasitized females ≥ 10 (Table 1), there was no difference between the relative proportions of unparasitized females with egg sacs and parasitized females with egg sacs in 1986 (Chi-squares ≤ 0.106 , $df = 1$, continuity correction, $P \geq 0.744$) or 1987 (Chi-squares ≤ 0.544 , $df = 1$, continuity correction, $P \geq 0.461$). It is of course impossible to determine from my data whether parasitism may have adversely affected fecundity via decreased egg production or may have rendered females more susceptible to mortality prior to ovipositing. However, these data

Table 1.—Morph frequencies and incidence of mite parasitism among coastal Maine populations of mature female *E. ovata*. LIN = *lineata* phenotype; RED = *redimita* phenotype; OVA = *ovata* phenotype; ES = total number of females with egg sacs; "M" refers to number of individuals with mites in each category; %M = frequency of parasitism for sample size *N*. Egg sac data given only for populations with total #M ≥ 10 .

POPN/YR	LIN		RED		OVA		Combined			ES	
	<i>N</i>	(M)	<i>N</i>	(M)	<i>N</i>	(M)	<i>N</i>	(M)	(%M)	<i>N</i>	(M)
GCP/86	181	(12)	5	(0)	0	(0)	186	(12)	(0.065)	184	(12)
SS/86	221	(1)	3	(0)	0	(0)	224	(1)	(0.004)		
MH/86	197	(2)	6	(0)	0	(0)	203	(2)	(0.010)		
MH/87	170	(1)	4	(0)	0	(0)	174	(1)	(0.006)		
BPP/86	202	(23)	4	(0)	0	(0)	206	(23)	(0.112)	206	(23)
BPP/87	196	(21)	3	(0)	0	(0)	199	(21)	(0.106)	131	(10)
DC/87	2485	(4)	203	(0)	87	(0)	2775	(4)	(0.001)		
DM/86	155	(9)	17	(1)	5	(0)	177	(10)	(0.056)	175	(10)
DM/87	194	(24)	29	(7)	4	(1)	227	(32)	(0.141)	152	(24)
NL1/86	840	(35)	189	(10)	75	(6)	1104	(51)	(0.046)	1088	(48)
NL1/87	1535	(53)	244	(9)	138	(8)	1917	(70)	(0.037)	1038	(44)
NL2/86	435	(82)	105	(29)	35	(8)	575	(119)	(0.207)	543	(106)
NL2/87	481	(54)	93	(8)	55	(11)	629	(73)	(0.116)	305	(40)
NL3/86	204	(2)	63	(0)	27	(0)	294	(2)	(0.007)		
NL3/87	253	(3)	47	(2)	26	(2)	326	(7)	(0.021)		
MP/86	238	(25)	25	(1)	4	(0)	267	(26)	(0.097)	263	(26)
MP/87	576	(67)	59	(10)	17	(0)	652	(77)	(0.118)	369	(46)
OCR1/86	127	(3)	32	(2)	4	(0)	163	(5)	(0.031)		
OCR2/86	59	(2)	15	(0)	1	(0)	75	(2)	(0.027)		
OCR4/86	38	(2)	7	(0)	2	(0)	47	(2)	(0.043)		
J/86	209	(1)	13	(0)	2	(0)	224	(1)	(0.004)		
C/87	194	(0)	38	(2)	9	(0)	241	(2)	(0.008)		

suggest that parasitism by *Parasitengona* larvae to not provide a selective mechanism for maintenance of color polymorphism in coastal Maine *E. ovata* populations.

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NOCTURNAL PREDATION BY *MISUMENA VATIA* (ARANEAE, THOMISIDAE)

Spiders of the family Thomisidae are typically small ground or vegetation inhabitants which capture their prey by ambush and do not spin webs (Gertsch 1979). Because of their dependence on vision, thomisids are primarily active during the day (Foelix 1982). The crab spider *Misumena vatia* (Clerck) is one of the most abundant and widely distributed of the "flower spiders" in North America. It is commonly observed during the day on flowers such as goldenrod in the late summer and fall (Kaston 1978). *Misumena vatia* has been reported to feed in the daytime on dragonflies and butterflies (Lovell 1915), as well as on bumblebees, honeybees, hoverflies, and various unidentified insects (Morse 1979). To our knowledge, Morse (1981) presents the only record of nocturnal predation. He does not indicate when in the nocturnal period it occurred or the species of the "moth" prey. While conducting nocturnal sampling of cotton insects, we occasionally observed evidence of predation by *M. vatia*. Although these observations are preliminary, we believe they provide further evidence for the nocturnal activities of this spider.

Observations were conducted in a 1-ha fallow crimson clover field in Washington Co., Mississippi, from 4-9 September 1987. Weather conditions during this period were moderate; temperatures ranged between lows of 16°C and highs of 33°C; there was no precipitation; incidence of solar radiation averaged over 400 langleys/day; and the wind blew occasionally (0-10 km/h) from the southwest. The region is largely agricultural, with nearly all the surface area covered by catfish ponds, roads and drainage ditches, and row crops including: cotton, corn, soybeans, grain sorghum and rice. This particular field had been undisturbed since spring and was overgrown with Johnsongrass. Scattered throughout the field and protruding above the canopy were isolated individuals of the Common Sunflower, *Helianthus annuus* L. (Compositae). These plants were 1.7-2.0 m tall and contained 8-12 inflorescences each, from 0.3 to 2.0 m above the ground. One particular plant, the only one in full bloom, was examined daily at

Table 1.—Prey of *Misumena vatia* and time observed.

Date	Time	Taxon of prey	Prey stage
4 Sept.	2100	<i>Trichoplusia ni</i> (Hubner) (Lepidoptera: Noctuidae)	adult
	2130	<i>T. ni</i>	adult
	2200	<i>Diabrotica undecimpunctata howardi</i> Barber (Coleoptera: Chrysomelidae)	adult
	2230	<i>Colomychus talis</i> (Grt.) (Lepidoptera: Pyralidae)	adult
	2300	<i>T. ni</i>	adult
9 Sept.	2100	<i>T. ni</i>	adult
	2130	<i>T. ni</i>	adult
	2230	<i>D. undec. howardi</i>	adult

0700-0800 for the presence of *M. vatia* and at no time were more than two individuals detected, none with prey. This same plant, when observed after dark, contained as many as nine individuals, some with prey.

Local sunset during early September is approximately 1915 with moonrise occurring at 1500 on 4 Sept. and 2130 on 9 Sept. On both nights from 2000-2400, the *Helianthus* plant was visually searched for spiders, with the aid of a red-filtered headlamp. Numbered tape markers were attached to a stem within 10 cm of each individual. At 30-min intervals each spider was examined and removed from the plant if prey had been captured.

On 4 Sept., nine *M. vatia* were observed on one *Helianthus* plant, with five capturing prey between 2000 and 2400 (Table 1). On 9 Sept., six *M. vatia* were observed on the same plant, with three individuals obtaining prey during the observation period. All were observed as solitary occupants of an inflorescence, positioned with the center of the vertically oriented flower and facing downward, with the first two pair of legs spread wide in an "alert" posture.

A cursory comparison of diurnal and nocturnal observations at *Helianthus* during early September indicated considerably more night-time insect activity. Not only were the inflorescences attractive to various insects, but moths were also observed feeding at the extra-floral nectaries located on the petal bracts. *Misumena vatia* appears to have responded to this nocturnal peak in prey activity by expanding its typical diurnal predatory activity into at least the early portion of the night. This same general phenomenon was reported by Morse (1981), who demonstrated that nocturnal predation by *M. vatia* on milkweed, but not on goldenrod, was associated with high nocturnal insect activity on milkweed compared to low nocturnal activity on goldenrod. We therefore suggest that *M. vatia* does not depend on visual cues and has the ability to be a successful predator outside the typical thomisid activity period.

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A *SATHROCHTHONIUS* NORTH OF THE EQUATOR (PSEUDOSCORPIONIDA, CHTHONIIDAE)

The genus *Sathrochthonius* was established by J. C. Chamberlin (1962) on the basis of *S. tuena*, n. sp., from near Sydney, N.S.W., Australia. Subsequently, 2 other species were described from Australia (*S. crassidens* Beier, 1966a, from New South Wales, and *S. webbi* Muchmore, 1982, from Queensland), 1 species from New Caledonia (*S. kaltenbachii* Beier, 1966b), and 2 species from New Zealand (*S. maoricus* and *S. insulanus* Beier, 1976). Unexpectedly, a species was discovered in central Chile (*S. pefauri* Vitali-di Castri, 1974); and now a new *Sathrochthonius* has been found in southeastern Venezuela at latitude 5°N.

Sathrochthonius venezuelanus, new species

Figs. 1-3

Type data.—Holotype female (WM7067.01001), from VENEZUELA: Bolivar, La Gran Sabana, 9 km from Chivatón Hotel toward Kavanayén (about 5°30'N, 61°30'W), (1370 m), 29 June 1987, (M. A. Ivie), under bark of dead tree; deposited in Florida State Collection of Arthropods, Gainesville.

Diagnosis.—A 2-eyed species much like *S. pefauri* but smaller (palpal femur < 0.45 mm), with a distinct spinneret on the movable finger of the chelicera, and with no trace of coxal spines or granulations on pedal coxae.

Description of female holotype (male unknown).—Generally typical of the genus (Chamberlin 1962:303). Body and appendages pale tan. Carapace mostly smooth, finely reticulated laterally; entire anterior margin finely denticulated, slightly depressed at middle, with no obvious epistome; 2 corneate eyes; chaetotaxy 6-4-4-2-2. Coxal area typical except that there are no coxal spines and no granulations on any of the coxae; chaetotaxy 2-2-3-2-6:2-6(7):2-8:2-9; intercoxal tubercle bisetose. Abdomen typical; tergites and sternites smooth; tergal chaetotaxy 6:6:8:9:9:8:8:8:8:8:T2T:0; sternal chaetotaxy 10:(3)10(3):(2)10(2):11:11:11:12:9:10:0:2.

Chelicera 0.65 as long as carapace; hand with 6 setae; flagellum of about 10 pinnate setae; spinneret a distinct projection from movable finger (Fig. 1); serrula exterior of about 18 blades.

Palp robust (Fig. 2); femur 3.15, tibia 1.9, and chela 3.3 times as long as broad; hand 1.6 times as long as deep; movable finger 1.16 times as long as hand. Surfaces smooth except for small granules on bases of chelal fingers and some elevated setal areoles on femur and trochanter. Trichobothria as shown in Fig. 3.



Figures 1-3.—*Sathrochthonius venezuelanus*, n. sp., holotype: 1, tip of movable finger of chelicera; 2, right palp, dorsal view; 3, left chela, lateral view.

Fixed chelal finger with 37 teeth, all cusped; movable finger with 39 teeth, cusped distally and proximally but rounded in middle of row; fixed finger with an accessory denticle on internal surface near distal end.

Legs typical. Leg IV with entire femur 2.6 and tibia 3.65 times as long as deep; tactile seta near proximal end of both basitarsus and telotarsus; telotarsus lacking a tooth at distal end of upper margin.

Measurements (mm).—Body length 1.30. Carapace 0.45/0.43. Palpal trochanter 0.215/0.125; femur 0.41/0.13; tibia 0.245/0.13; chela 0.63/0.19; hand 0.32/0.20; movable finger 0.37 long. Leg IV: entire femur 0.40/0.155; tibia 0.31/0.085; basitarsus 0.14/0.06; telotarsus 0.245/0.05.

Remarks.—It was a great surprise to find this specimen in a collection from Venezuela, as *Sathrochthonius* has been known in the Western Hemisphere only from central Chile, well south of the equator. Evidently the genus is distributed over a great area of South America, not confined to the southwestern part, to the *Nothofagus* forest, as suggested by Vitali-di Castri (1973, 1974). Additional collecting may well show that *Sathrochthonius*, like *Austrochthonius*, is represented in South Africa as well (cf. Vitali-di Castri, 1973).

Sathrochthonius venezuelanus does not possess the small tooth at the end of the upper margin of telotarsus IV as described by Vitali-di Castri for *S. pefauri* (1974:199 and fig. 10). However, reexamination of some paratypes of *S. webbi* Muchmore (1982) reveals the presence of such a projection in that Australian species. Here, the "tooth" is actually a spinelike projection of the rim of the areole of the large terminal seta of the upper tarsal margin, not an extension of the tarsal surface itself. Such an elaboration of the terminal areole is more or less developed in some other chthoniids as well (personal observation). And it is

similar to the projection of the areoles of the coxal spines in the North American genera *Apochthonius* and *Kleptochthonius* (cf. Benedict and Malcolm 1973).

I am much indebted to Michael A. Ivie for providing the material on which this description is based.

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APHID PREDATION BY HARVESTMEN IN POTATO FIELDS IN SCOTLAND

Several species of aphids damage potatoes in Scotland. Dixon (1986) has studied the natural enemies of potato aphids, paying particular attention to polyphagous predators like harvestmen, spiders and ground beetles. The harvestmen, *Leiobunum rotundum* (Latreille) (Todd 1950) and *Phalangium opilio* Linné (Bristowe 1949) are known to prey on aphids, but little information exists on harvestmen as predators of aphids on potatoes. This paper reports on the predation of aphids by harvestmen in potato fields in Scotland.

Harvestmen were caught in pitfall traps during the summers of 1983-85 inclusive in fields of potatoes (cv. Maris Piper) near Edinburgh, Scotland. Pitfall traps were clear polystyrene containers (perimeter: 25 cm) placed in the potato furrows with their rims at soil level. Traps were emptied weekly. Forty-five ml of 10% formalin and a drop of liquid detergent were added to each trap at each

Table 1.—Total numbers of harvestmen caught in pitfall traps in Scottish potato fields during 1983 and 1984.

Species	1983	1984
<i>Phalangium opilio</i> Linné	65	61
<i>Opilio saxatilis</i> C. L. Koch	47	3
<i>Mitopus morio</i> (Fabricius)	16	7
<i>Paroligolophus agrestis</i> (Meade)	11	0
Immature harvestmen	1	19
<i>Leiobunum rotundum</i> (Latreille)	1	1
<i>Oligolophus tridens</i> (C. L. Koch)	1	0
<i>Opilio parietinus</i> (DeGeer)	1	0

sampling occasion. One hundred and twenty traps were spaced over 1.3 ha in 1983, but this trapping intensity was too time consuming and in each of 1984 and 1985, 56 traps were used in 2.0 ha.

Harvestmen were dissected under a binocular microscope and stomachs with attached gastric caecae were removed, placed on slides in 40% glycerine (after Loughridge and Luff 1983), and examined at 100X bright-field. Aphid remains were counted and identified to species (*Macrosiphum euphorbiae* (Thomas), *Myzus persicae* (Sulzer) (Homoptera: Aphididae)) where possible. All harvestmen were dissected except during late summer when aphids were not present in the field.

Seven species of harvestmen were trapped during 1983 and 1984, but none in 1985 (Table 1). Of a total of 233 individuals, 54% were *Phalangium opilio*, a long-legged, highly active species which usually inhabits woodland and bushes (Sankey and Savory 1974). Dempster (1967) suggested that *P. opilio* was an important predator of *Pieris rapae* (L.) (Lepidoptera: Pieridae) in Brussel sprout crops. This harvestmen has been recorded from potato fields in England (Foster 1972). The data for other species trapped are combined over time because the numbers trapped were low. *Phalangium opilio* was present over most of the summer, but *Opilio saxatilis*, the next most frequently trapped species, occurred almost entirely in September. Although populations were probably underestimated by pitfall trapping, the method will have indicated which species were present. The usual methods of sampling harvestmen include beating and sweeping foliage or using funnels (Berlese, Tullgren) to assess soil and litter samples (Sankey and Savory 1974).

Of the species trapped in potato fields, all contained aphid remains except the single *Oligolophus tridens*. Fifty-four percent of 113 *P. opilio* examined, had eaten aphids. The maximum number of aphids found in a harvestman was in a *P. opilio* which contained at least five (30 legs, 4 siphunculi, and 3 rostra).

Opiliones have been neglected and probably undervalued as predators of crop pests. The present study has shown that several species prey on aphids in potato crops. Harvestmen may have great potential in natural pest control and warrant further research.

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NUEVAS ESPECIES DEL GENERO *PHILODROMUS* (ARANEAE, PHILODROMIDAE) DE LA REGION DEL CABO, B.C.S., MEXICO

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ABSTRACT

Two new species of the genus *Philodromus infuscatus* group. *P. jimredneri*, *P. pericu* and the male of *P. coachellae* from the Cape Region, Baja California Sur, México, are described and illustrated.

RESUMEN

Se describen e ilustran dos especies nuevas del género *Philodromus*, grupo *infuscatus*: *P. jimredneri* y *P. pericu*, además el macho *P. coachellae* de la Región del Cabo, Baja California Sur, México.

INTRODUCCION

El grupo *infuscatus* del género *Philodromus* comprende 20 especies de arañas, la mayoría ampliamente distribuidas en las zonas áridas de Estados Unidos y México (Dondale y Redner 1969). De ellas, diez han sido citadas para la República Mexicana: *Philodromus pratariae* (Scheffer 1904), *P. pratarioides*, *P. separatus* Dondale y Redner 1969, *P. infectus* Dondale y Redner 1969, *P. pseudanomalus* Dondale y Redner 1969, *P. cavatus* Dondale y Redner 1969, *P. mexicanus* Dondale y Redner 1969 y *P. albicans* O. Pickard-Cambridge, 1897. (Bonnet 1958; Dondale y Redner op. cit.).

Banks (1898) en su trabajo sobre los arácnidos de Baja California y otras partes de México, señala "no haber encontrado representantes del género *Philodromus* en la fauna de la región del Cabo". Jiménez (1988) durante el estudio sobre las arañas de la "Reserva de la Biosfera Sierra de la Laguna", cita por primera vez a *P. coachellae* Schick, 1964 y *P. infuscatus utus* Chamberlin, 1921 para esta región.

En este trabajo se describen dos especies nuevas del grupo *infuscatus* y se dan a conocer los caracteres del macho de *P. coachellae* Schick. Estas arañas habitan la selva baja caducifolia y bosque de pino-encino de la Sierra de la Laguna y del matorral xerófilo del Comitán, Baja California Sur.

Philodromus jimredneri, especie nueva

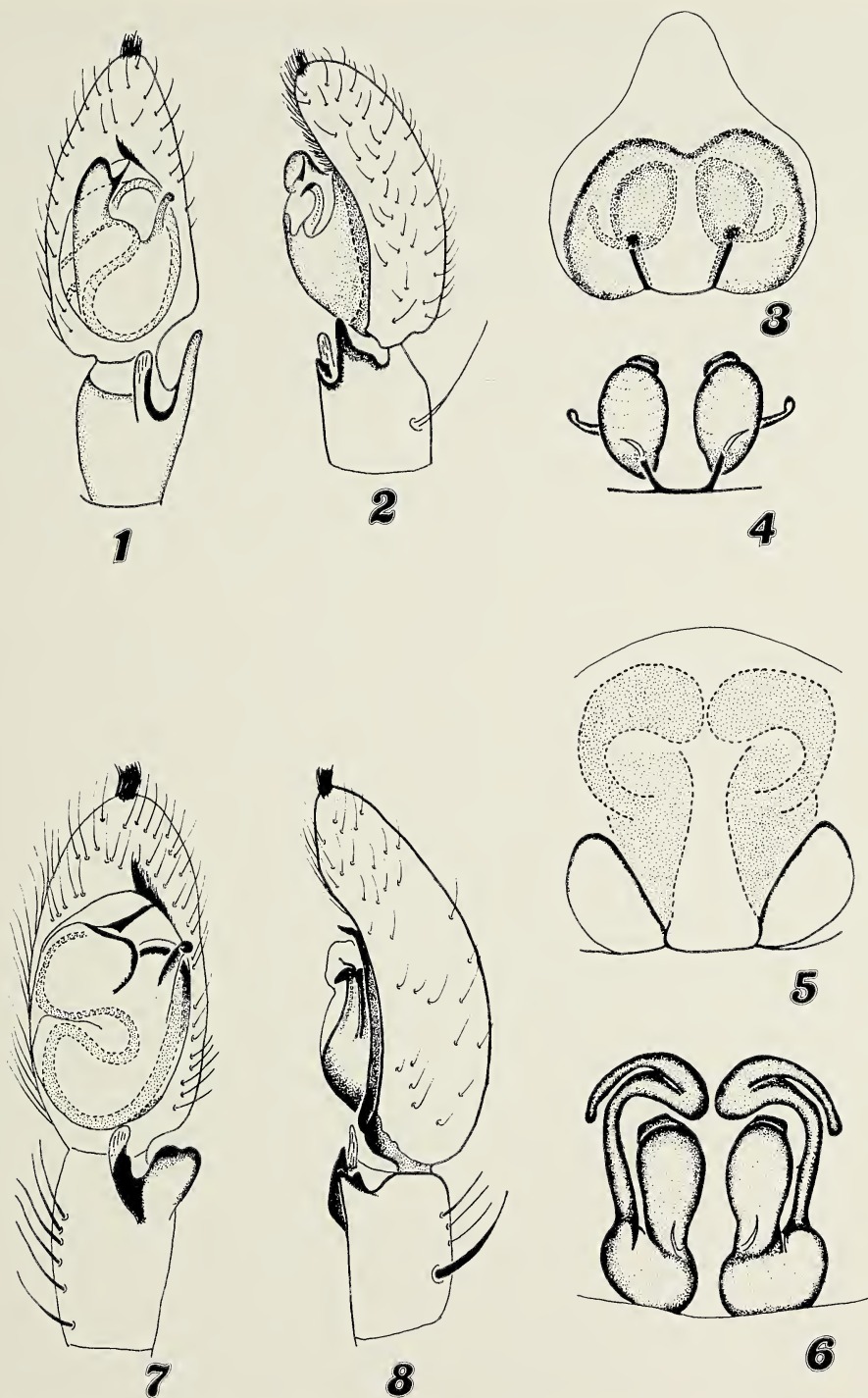
Figs. 1-4

Datos del tipo.—Holotipo macho recolectado en Comitán, Baja California Sur, matorral xerófilo, 17 de febrero 1987 (M. Jiménez) y los siguientes paratipos: una hembra y un macho, 24 de febrero 1987, 17 de febrero 1987 (M. Jiménez) todos de la misma localidad del tipo. El tipo será depositado en la colección del Laboratorio de Acarología (Facultad de Ciencias, Universidad Nacional Autónoma de México); los paratipos serán depositados en la colección aracnológica del Centro de Investigaciones Biológicas de Baja California Sur, A.C.

Macho.—Longitud total 2.72-3.25 mm, longitud del prosoma 1.12-1.25 mm y anchura 1.07-1.32 mm, femur II 1.87-2.02 mm (dos ejemplares). Prosoma dorsoventralmente aplanado, un poco más elevado al nivel de la coxa III, de color amarillo claro, moteado de café rojizo y blanco, con escasas sedas; area ocular con dos bandas medias oscuras que pasan entre los ojos medios posteriores, después del area ocular hay una mancha en forma de "V" bordeada de café en el extremo anterior; ojos posteriores en tubérculos grises. Patas pilosas, amarillo claro con anulaciones, lateralmente más oscuras y escasa escópula; fémur I 1.62-1.70 mm con tres macrosedas dorsales, dos prolaterales y tres retrolaterales; tibia I 1.32-1.35 mm con dos macrosedas prolaterales, dos retrolaterales y dos pares ventrales; basitarso I 1.12-1.15 mm con dos macrosedas prolaterales, dos retrolaterales y dos pares ventrales; tibia III 1.12-1.15 mm con una macroseda prolateral, una retrolateral y dos pares ventrales. Opistosoma ovalado, truncado anteriormente, con una fisura media, de color blanco, moteado de café grisáceo, con tres bandas transversas café en forma de "V" invertida, costados más oscuros y el vientre blanco. Tibia del pedipalpo con la apófisis ventral corta y delgada, apófisis retrolateral con dos dientes, uno corto y descansando sobre la apófisis ventral y el otro largo y puntiagudo; émbolo corto y recto; conductor curvo y delgado; cimbio sin proyección dorsal cónica y en la base con una prominencia angular en el lado retrolateral (Figs. 1 y 2).

Hembra.—Longitud total 3.67 mm, longitud del prosoma 1.17 mm y anchura 1.22 mm (un ejemplar). Estructura general similar a la del macho pero con coloración más clara; femur II 2.00 mm; femur I 1.65 mm con dos macrosedas dorsales, dos prolaterales, ninguna ventral; tibia I 1.65 mm con tres macrosedas prolaterales, tres retrolaterales y dos pares ventrales; basitarso I 1.17 mm con tres macrosedas prolaterales, tres retrolaterales y tres pares ventrales; tibia III 1.17 mm con una macroseda prolateral, una retrolateral, dos pares ventrales. Epiginio tan largo como ancho, con una ligera depresión y un septo medio ancho que va disminuyendo posteriormente (Fig. 3); espermatecas contiguas alargadas y ovales con un pequeño abultamiento en el margen anterior; conducto del órgano espermático delgado y corto, que surge en la parte media lateral del cuerpo principal; tubos de fertilización presentes (Fig. 4).

Discusion.—*Philodromus jimredneri* presenta características afines a *P. pseudanomalus* Dondale y Redner, pero difiere en lo siguiente: el émbolo es más corto, el conductor es más largo y curvo y el cuerpo principal de las espermatecas presenta abultamientos en las márgenes anteriores. Es menos parecida a *P. anomalus* Gertsch, porque el lóbulo de la base del émbolo, es menos agudo y el



Figures 1-8.—Especies del género *Philodromus*: 1-4, *Philodromus jimredneri* sp. nov.; 1, pedipalpo, vista ventral; 2, pedipalpo, vista lateral; 3, epiginio, vista ventral; 4, epiginio vista dorsal; 5, 6, *Philodromus pericu* sp. nov.; 5, epiginio, vista ventral; 6, epiginio, vista dorsal; 7, 8, *Philodromus coachellae* Schick, 1965; 7, pedipalpo, vista ventral; 8, pedipalpo, vista lateral.

conducto de los órganos espermáticos surge en la mitad media lateral del cuerpo principal de las espermatecas.

Distribución.—Conocida sólo para la localidad del tipo.

Etimología.—Esta especie está dedicada al Sr. James Redner del Biosystematics Research Centre, Ottawa, Canada, como reconocimiento a su gran labor dentro del estudio de las Philodromidae y en agradecimiento por la ayuda brindada.

Philodromus pericu, nueva especie

Figs. 5, 6

Datos del tipo.—Holotipo hembra recolectado en la Sierra de la Laguna, Cañon de la Zorra, selva baja caducifolia, 840 m, 6 de marzo 1986 (F. Cota) y los siguientes paratipos: dos hembras, 1685 m, 15 de enero 1988 (F. Cota), 840 m 17 de enero 1988 (V. Roth) todos de la misma localidad del tipo. El tipo será depositado en la Colección del Laboratorio de Acarología, (Faculta de Ciencias, Universidad Nacional Autónoma de México); un paratipo será depositado en el Centro de Investigaciones Biológicas de Baja California Sur, A.C. y otro en el Biosystematic Research Centre, Ottawa, Canada.

Hembra.—Longitud total 3.42-3.95 mm; longitud y ancho del prosoma 1.30-1.45 mm, femur II 2.00-2.32 mm (tres ejemplares). Prosoma dorsoventralmente aplanado, un poco más elevado a nivel de coxa III, amarillo café, finamente moteado con una banda media longitudinal blanca, márgenes negros y frente con una línea blanca que continúa hacia los costados a nivel de coxa II; ojos laterales en tubérculos grises, los lateroposteriores sobre una mancha blanca; esternón, labio y enditos blancos con sedas hialinas. Patas claras con bandas oscuras laterales, patelas más oscuras y fémures con macrosedas sobre manchas oscuras; femur I 1.70-1.82 mm con dos macrosedas dorsales, dos prolaterales, dos retrolaterales y dos distodorsales; tibia I 1.37-1.52 mm, sin macrosedas dorsales, tres prolaterales, tres retrolaterales y dos pares ventrales; basitarso I 1.17-1.45 mm con tres macrosedas prolaterales, tres retrolaterales y tres pares ventrales; tibia III 1.12-1.17 mm con dos macrosedas prolaterales, dos retrolaterales y dos pares ventrales. Opistosoma de forma ovalada y larga, región cardíaca con una banda media dorsal que se ensancha y se interrumpe formando tres líneas transversas en forma de "V" invertida, costados café oscuro salpicados de blanco con una banda blanca que se interrumpe a la mitad del opistosoma; vientre blanco. Epiginio con un septo medio amplio truncado posteriormente; atrio poco profundo con márgenes laterales redondos (Fig. 5), cuerpo principal de la espermateca alargado y sin lobulaciones y con abultamientos en su margen anterior; conducto del órgano espermático muy largo y delgado que se dobla hacia la parte anterior (Fig. 6).

Discusion.—*Philodromus pericu* es similar a *P. pratairoides* Dondale y Redner, pero difiere en que presenta las patas con bandas laterales y la coloración del cuerpo es más oscura; el septo medio del epiginio es truncado posteriormente, el conducto del órgano espermático es más delgado y el cuerpo principal de las espermatecas no es lobulado y presenta abultamientos anteriores.

Distribución.—Conocida sólo para la localidad del tipo.

Etimología.—El nombre es derivado de la tribu "pericu", indios nativos de Baja California Sur.

Philodromus coachellae Schick, 1965

Figs. 7, 8

Philodromus coachellae Schick 1965. Dondale y Redner 1969 Canadian Entomol. 101:933, figs. 58 y 59 hembra.

Datos del macho.—Nueve machos colectados en varias altitudes: 840 m, 4 octubre de 1986, 1 noviembre de 1986, 786 m, 29 octubre de 1987; 420 m, 1 noviembre de 1987 (M. Jiménez y F. Cota cols.) Los especímenes serán depositados en la Colección aracnológica del Laboratorio de Acarología (Facultad de Ciencias, Universidad Nacional autónoma de México) así como representantes en el Centro de Investigaciones Biológicas de Baja California Sur, A.C., en el Biosystematics Research Centre, Ottawa, Canada y en la colección particular de la autora.

Macho.—Longitud total 2.50-3.80 mm, longitud del prosoma 1.20-1.62 mm y anchura 1.22-1.57 mm (9 ejemplares), femur II 2.32-3.02 mm. Prosoma amarillo con una mancha clara en forma de "V" en frente del surco dorsal; áreas laterales moteadas y con dos manchas blancas a nivel de coxas I y II; con escasas sedas cortas y fuertes; márgenes oscuros; ojos encerrados en círculos blancos sobre tubérculos grises; labio y enditos amarillos y esternón blanco salpicado con pequeñas manchas oscuras en sus márgenes. Patas largas, delgadas y moteadas, fémures más claros y tarsos oscuros, con escasa escópula; fémur I 1.80-2.57 mm, con tres macrosedas dorsales, tres prolaterales, tres retrolaterales; tibia I 1.62-2.10 mm, con una macroseda dorsal, tres prolaterales, tres retrolaterales, dos pares ventrales; basitarso I 1.37-1.82 mm, con tres macrosedas prolaterales, tres retrolaterales y tres pares ventrales; tibia III 1.17-1.50 mm con una macroseda dorsal, dos prolaterales, tres retrolaterales y dos pares ventrales. Opistosoma gris, dos veces más largo que ancho sin sedas, truncado en el frente, con una muesca media anterior; dorso con una mancha clara en la región cardíaca, finamente moteado de café rojizo, con una banda ancha transversal posterior blanca; costados blancos con líneas oscuras inclinadas, vientre claro. Tibia del pedipalpo más larga que ancha; apófisis ventral delgada y poco esclerosada y más larga que la apófisis retrolateral, esta última presenta dos dientes, el más largo descansa sobre la apófisis ventral y el corto presenta una cúspide bifida; émbolo corto y abultado en su base con una punta delgada y en ocasiones engrosada, que se aloja lejos del conductor que es delgado pequeño y con el extremo curvo; cimbio sin saliente angular en el lado retrolateral y sin proyección cónica dorsal en la base (Figs. 7-8).

Discusion.—Los machos de *Philodromus coachellae* Schick se parecen a los de *P. mexicanus* Dondale y Redner, en que ambos tiene el cuerpo alargado y delgado, el conductor del pedipalpo es delgado y largo, pero difieren en que la primera especie presenta el émbolo más delgado y con la punta recta, la apófisis retrolateral bicúspide y la fórmula de las macrosedas de las patas es diferente. El macho descrito como *P. coachellae* ha sido colectado con las hembras de ésta especie en varias ocasiones.

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VARIACION RELATIVA DE CARACTERES SOMATICOS Y GENITALES EN *GRAMMOSTOLA MOLLICOMA* (ARANEAE, THERAPHOSIDAE)

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ABSTRACT

A quantitative analysis of somatic and genital characters on a sample of *Grammostola mollicoma* (Ausserer, 1875) showed higher intraspecific variation in genitalic than somatic characters, especially in females. Experimental copulation within a subsample confirmed that all were the same species. These results seems to be uncommon in spiders and may result from: i) female moulting after maturity ecdysis; ii) allometric growth of spermathecae; iii) multiple sexual selection by female choice (according to female size) and its effects on male genitalic evolution.

RESUMEN

Un análisis cuantitativo de caracteres somáticos y genitales realizado en una muestra de *Grammostola mollicoma* (Ausserer, 1875) mostró una variación intraespecífica mayor en caracteres genitales que en los somáticos, especialmente en hembras. Cópulas experimentales realizadas en una submuestra confirmaron la coespecificidad. Estos resultados parecen ser poco comunes en arañas y podrían deberse a: i) que las hembras continúan mudando después de adultas; ii) crecimiento alométrico de las espermatecas; iii) selección sexual múltiple por elección de la hembra (condicionada por el tamaño de la hembra) y sus efectos sobre la evolución de la genitalia de los machos.

INTRODUCCION

El género *Grammostola* Simon 1892, incluye especies de gran tamaño y de distribución exclusivamente sudamericana. Este género ha sido utilizado repetidas veces para estudiar el valor de caracteres sistemáticos de Mygalomorphae (Bucherl 1951, 1957; Schiapelli y G. de Pikelin 1960, 1962a, b; G. de Pikelin y Schiapelli 1969).

En los últimos 40 años han predominado dos tendencias controvertidas en la utilización de caracteres considerados específicos en *Grammostola*: (i) el uso de caracteres morfométricos somáticos (Bucherl 1951) y (ii) el uso de caracteres morfológicos genitales (Schiapelli y G. de Pikelin 1960).

El argumento más utilizado en la literatura para dilucidar el valor específico de los caracteres en *Grammostola* ha sido su variabilidad. Sin embargo, los estudios de Bucherl (1951) y Schiapelli y G. de Pikelin (1960, 1962), se han realizado en individuos cuya coespecificidad es dudosa o en taxones de estabilidad discutida. Otros inconvenientes detectados en trabajos previos es que no presentan

resultados cuantitativos de variación ni vinculan sus resultados de caracteres genitales con las hipótesis clásicas de aislamiento reproductor.

La variación relativa de caracteres genitales y somáticos ha sido objeto de estudios recientes en Araneae (e.g., Vollrath 1980; Coyle 1985; Blasco-Feliu 1986) surgiendo interpretaciones explicativas novedosas (Eberhard 1983, 1985). Tales aportes dan elementos adicionales para la interpretación de la variación de caracteres en *Grammostola* que no han podido tenerse en cuenta en el pasado.

En este trabajo se estudia la variabilidad de dos grupos de caracteres (genitales y somáticos) en una muestra de *G. mollicoma* de Uruguay y Sur de Brasil. Diez cópulas experimentales en una submuestra confirmaron la coespecificidad y permitieron el estudio detallado de la variación de genitales de los individuos que copularon. Los objetivos de este estudio son: i) confirmar el status específico de la muestra; ii) analizar la variabilidad intraespecífica de caracteres genitales y somáticos en *G. mollicoma*; iii) analizar el grado de asociación entre caracteres mediante técnicas de agrupamiento y iv) agregar elementos para evaluar las hipótesis de selección sexual.

Los resultados de este estudio permitirán establecer una base más sólida y objetiva de discusión, con utilidad potencial en la sistemática de este género y en Theraphosidae.

MATERIAL Y METODOS

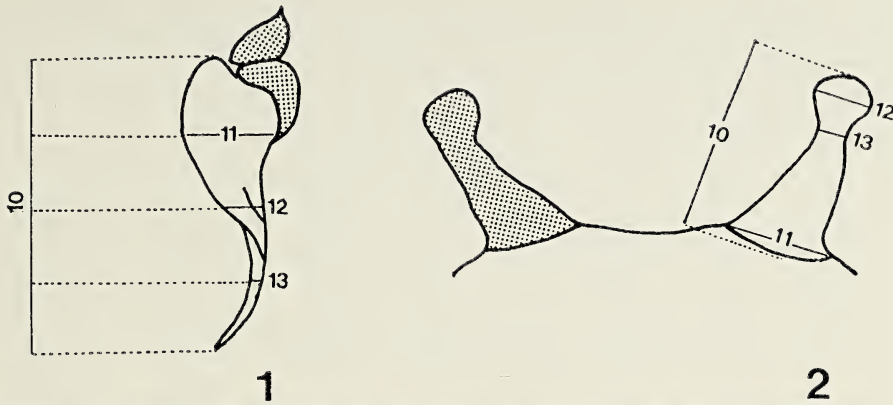
Cuarenta y dos individuos (24 machos y 18 hembras) de *G. mollicoma* (Ausserer, 1875), procedentes de Uruguay y Sur de Brasil (al sur del paralelo 28 S) fueron examinados y depositados en las colecciones del Museo Nacional de Historia Natural, Montevideo, de Instituto Butantan (IB) Sao Paulo. Los ejemplares fueron determinados por comparación con el material típico (holotipo macho y paratipo hembra, depositados en el British Museum of Natural History [BMNH], Londres).

Una submuestra de 4 machos y 5 hembras fueron utilizados en experiencias de comportamiento sexual. Las observaciones se realizaron en recipientes de vidrio de 39x16x20 cm, con una capa de arena en el fondo, registrando el relato por grabación magnetofónica. Durante las experiencias la temperatura del laboratorio varió entre 23 y 25°C.

Caracteres: Fueron registrados nueve caracteres somáticos: (1) longitud de pata I, (2) longitud de pata II, (3) longitud de pata III, (4) longitud de pata IV, (5) longitud de cefalotorax, (6) ancho máximo de cefalotorax; índices entre longitudes de : (7) pata I/pata IV, (8) cefalotorax/pata I, (9) cefalotorax/ pata IV.

Los caracteres genitales registrados en machos (Fig. 1) fueron: (10) longitud del bulbo, (11) ancho del bulbo a $\frac{1}{4}$ de su longitud (comenzando desde su extremo basal), (12) ancho del bulbo a $\frac{1}{2}$ de su longitud, (13) ancho del bulbo a $\frac{3}{4}$ de su longitud (comenzando del extremo basal). Todos los anchos fueron tomados perpendicularmente a la longitud. Índices entre: (14) carácter 11/carácter 10, (15) carácter 12/carácter 10, (16) carácter 13/carácter 10.

Los caracteres genitales registrados en hembras (Fig. 2) fueron: (10) longitud de espermatecas, (11) ancho de la base de espermatecas, (12) ancho máximo del fundus, (13) cuello mínimo de espermatecas; índices entre: (14) carácter 11/carácter 10, (15) carácter 12/carácter 10, (16) carácter 13/carácter 10.



Figuras 1-2.—Bulbos y espermatecas de *G. mollicoma* mostrando las medidas tomadas, como se definen en el texto: 1, bulbo vista prolateral, con trama el esclerito I, en blanco escleritos I + II; 2, espermatecas (vista ventral), la trama indica el área glandular.

Las mediciones fueron realizadas con micrómetro ocular (apreciación 0.1 mm). Las patas fueron medidas artejo por artejo, por su parte media dorsal; tomándose en cuenta únicamente las partes esclerificadas. Otros caracteres fueron tomados de dibujos de todos los ejemplares, realizados con cámara clara y aumento fijo. Las medidas corresponden a bulbos y espermatecas izquierdos. En las espermatecas se tomó en cuenta particularmente el área glandular (De Carlo 1973), que fue dibujada (Fig. 2). Los términos de morfología de bulbo siguen a Kraus (1978, 1984).

Métodos estadísticos: Los estadísticos de los caracteres somáticos fueron estudiados por separado y luego comparados. Las medidas se compararon mediante test de *t* de Student para diferencia de medias, con restricciones para las varianzas (test de *F* de Snedecor). Los índices fueron comparados a partir del análisis de regresión entre los datos originales, mediante comparación de pendientes e interceptos de acuerdo a Phillips (1983). La variabilidad de caracteres fue comparada por el método de Lewontin (1966), y graficada en perfiles de variabilidad según Sokal y Braumann (1980).

Los caracteres no homologables (somáticos con genitales y genitales entre sexos) fueron comparados todos contra todos por el test de Lewontin (1966).

Se realizaron análisis de agrupamiento para caracteres, por separado para machos y hembras. Los fenogramas fueron elaborados a partir de una matriz de correlación múltiple entre caracteres (estandarizados por transformación logarítmica neperiana) y utilizando ligamiento promedio (UPGMA). Se tomaron los caracteres como OTUs (técnica R), lo que permite agrupar caracteres jerárquicamente sobre la base de su correlación, e inferir la información que brindan. Estos procedimientos siguen en líneas generales a Sneath y Sokal (1973) y Crisci y Armengol (1983). El programa de cómputos multivariantes utilizado fue el paquete PRESTA, desarrollado en el Centro Ramón y Cajal, España.

CARACTERES SOMATICOS

Las medidas (caracteres 1 a 6) presentaron diferencias significativas ($p < 0.05$) entre machos y hembras (Tabla 1).

Tabla 1.—Estadísticos de los caracteres somáticos y genitales en *Grammostola mollicoma*: Car. = número de carácter; \bar{X} = promedio; DT = desvío típico; CV = coeficiente de variabilidad; t = valor de t de Student calculado (a = para interceptos; b = para pendientes).

Car.	Machos (N = 24)			Hembras (N = 18)			t	P
	\bar{X}	DT	CV	\bar{X}	DT	CV		
1	62.59	4.76	7.61	57.16	5.76	10.06	3.25	<0.01
2	60.78	3.75	6.18	53.04	5.29	9.98	4.03	<0.01
3	57.10	4.64	8.13	50.68	4.86	9.60	4.32	<0.01
4	68.96	5.34	7.75	62.02	5.89	9.50	3.93	<0.01
5	19.67	1.71	8.71	22.37	2.66	11.88	3.76	<0.01
6	18.14	1.76	9.72	20.17	2.47	12.24	2.97	<0.01
7	0.91	0.05	5.02	0.92	0.02	2.65	14.89 ^a	<0.001
							14.51 ^b	<0.001
8	0.31	0.01	4.25	0.39	0.01	3.62	4.65 ^a	<0.001
							0.19 ^b	0.90-0.80
9	0.29	0.02	7.82	0.36	0.02	5.12	5.14 ^a	<0.001
							1.12 ^b	0.30-0.20
10	5.20	0.11	10.42	1.38	0.28	20.11		
11	1.52	0.14	9.38	0.80	0.25	31.02		
12	0.85	0.11	13.37	0.46	0.11	24.58		
13	0.23	0.04	17.08	0.27	0.39	14.52		
14	0.29	0.02	7.82	0.60	0.13	21.71		
15	0.17	0.01	13.79	0.34	0.07	20.16		
16	0.05	0.01	15.65	0.20	0.04	18.18		

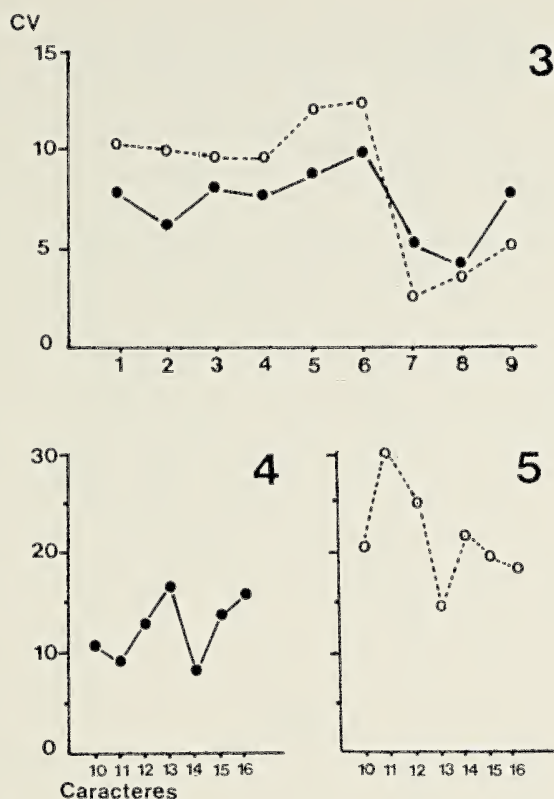
Los análisis de regresión entre los datos originales utilizados para los índices rechazaron la hipótesis nula $b = 0$ ($p < 0.05$). Los índices (caracteres 7 a 9) mostraron diferencias estadísticamente significativas entre machos y hembras en la comparación de interceptos ($p < 0.001$). La comparación de pendientes (Tabla 1) evidenció diferencias significativas entre sexos en el carácter 7 ($p < 0.001$) pero no en los caracteres 8 y 9 ($p > 0.20$).

Los caracteres 1 a 6 presentaron mayores CVs en las hembras que en los machos (Fig. 3, Tabla 1). Los caracteres 7 a 9 (índices) presentaron CVs menores en las hembras que en los machos (Fig. 3, Tabla 1). Al comparar la variabilidad de caracteres somáticos entre sexos, usando el test de Lewontin (1966), las diferencias no resultaron ser estadísticamente significativas ($p > 0.05$).

CARACTERES GENITALES

1. Espermatecas.—Las espermatecas de todas las hembras de *G. mollicoma* estudiadas comparten un mismo patrón morfológico: presentan un ápice (fundus) globuloso a subglobuloso y un conducto más o menos curvado, que se ensancha gradualmente en sentido basal. Dentro de este patrón morfológico se observó un amplio rango de variación continua intraespecífica (Fig. 6). Dicha variación fue evidenciada por los altos CVs de los caracteres 10 a 16 (Tabla 1, Fig. 5).

2. Bulbos.—Los bulbos de los individuos de *G. mollicoma* presentaron un mismo patrón morfológico pero con ciertas variaciones (Fig. 7). La región proximal (esclerito I) es fusiforme y espiralada; la región distal (escleritos II + III) presenta forma subcónica, terminada en un estilo largo y fino (Fig. 1). El surco de la "zona frágil" ("weak zone" de Kraus 1978) es aproximadamente



Figuras 3-5.—Perfiles de variabilidad (*sensu*: Sokal y Braumann 1980) de los caracteres estudiados: 3, caracteres somáticos (● machos, ○ hembras); 4, caracteres genitales de machos; 5, caracteres genitales de hembras.

perpendicular al eje mayor del bulbo. La región basal del estilo presenta una aleta conspicua.

3. Comparación de bulbos y espermatecas.—La variación de caracteres genitales de machos y hembras fue comparada (todos contra todos) utilizando el método de Lewontin (1966). De 49 comparaciones realizadas, 31 demostraron

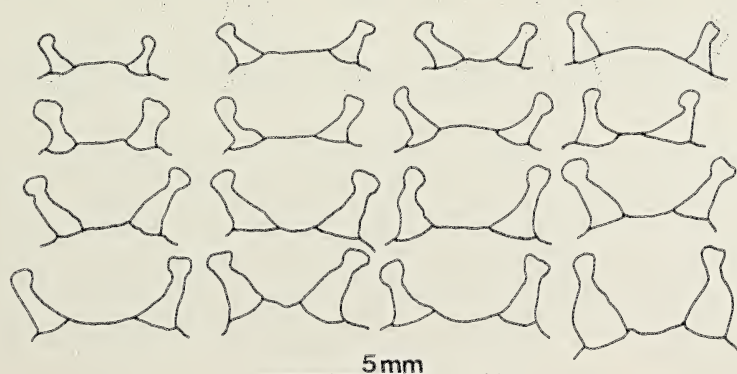


Figura 6.—Espermatecas de hembras de la muestra de *G. mollicoma* estudiada, vista ventral.

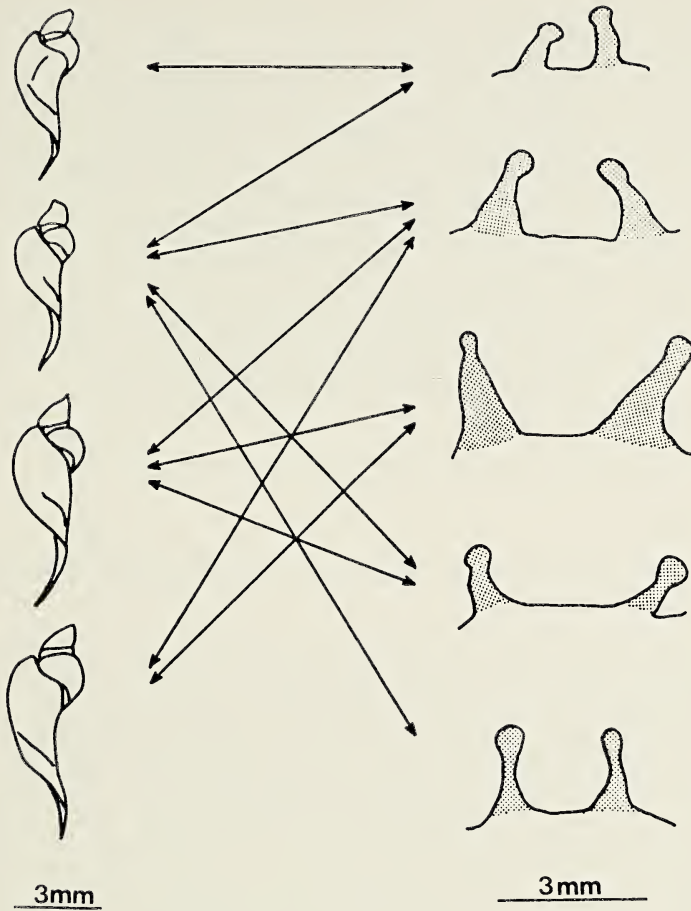


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Figura 7.—Bulbos izquierdos de machos de la muestra de *G. mollicoma* estudiada, vista prolateral.

una variabilidad significativamente mayor ($p < 0.05$) en los caracteres genitales de hembras que de machos y 18 no demostraron diferencias significativas ($p > 0.05$). Las comparaciones que no demostraron diferencias significativas de variabilidad fueron: carácter 10 de hembras con 12, 13, 15 y 16 de machos; 13 de hembras con 10, 12, 13, 15 y 16 de machos; 14 de hembras con 13 de machos; 15 de hembras con 12, 13, 15 y 16 de machos; 16 de hembras con 12, 13, 15 y 16 de machos. Coincidentemente estas comparaciones implican a los caracteres genitales más variables en los machos (12, 13, 15, 16) y menos variables en las hembras (10, 13, 14, 15 y 16) (Figs. 4 y 5).

4. Estudio experimental.—Se obtuvieron 10 cópulas experimentales entre 4 machos y 5 hembras de *G. mollicoma* (Fig. 8). Las uniones de individuos mediante cópulas sustentó con mayor grado de certeza su coespecificidad (aunque no pudo determinarse si ocurrió inseminación y fecundación). El estudio detallado de las espermatecas de las hembras que copularon permitió confirmar la extrema variabilidad observada en el material muerto. Estas experiencias sugieren que tales variaciones no corresponden a diferencias interespecíficas, ya que son observables aún entre hembras que copularon con el mismo macho. Los bulbos de los machos que copularon presentaron una variabilidad similar a lo observado en el material muerto.



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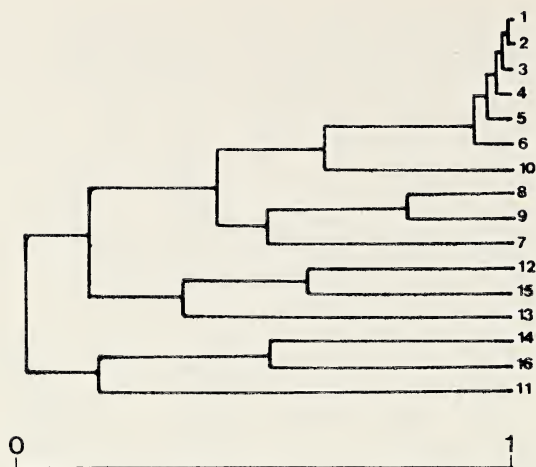
Figura 8.—Esquema de morfología de bulbos y espermatecas de una submuestra de *G. mollicoma*. Las flechas unen los individuos que copularon entre sí. La trama indica el área glandular.

COMPARACION DE CARACTERES SOMATICOS Y GENITALES

1. Comparación de variaciones.—La variación de todos los caracteres genitales fue comparada con la variación de todos los caracteres somáticos en hembras y machos.

En hembras; de 63 comparaciones realizadas, 57 demostraron una variabilidad significativamente mayor ($p < 0.05$) en caracteres genitales que en los caracteres somáticos y 6 comparaciones no demostraron diferencias significativas ($p > 0.05$). No demostraron diferencias significativas las comparaciones del carácter genital 13 (cuello mínimo de espermateca) con los caracteres somáticos 1 a 6. Coincidentemente, el carácter 13 presentó el menor valor de CV dentro de los caracteres genitales de las hembras (Fig. 5, Tabla 1).

En los machos; de 63 comparaciones realizadas, 41 demostraron una variabilidad significativamente mayor ($p < 0.05$) de los caracteres genitales que los somáticos y 22 comparaciones no demostraron diferencias significativas de variabilidad. No demostraron diferencias significativas las comparaciones de los



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Figura 9.—Fenograma de caracteres en hembras de *G. mollicoma*, técnica R, 16 caracteres, $n = 17$, coeficiente de correlación, UPGMA.

caracteres: 10 con 1 a 6 y 9; 11 con 1 a 6 y 9; 14 con 1 a 6 y 9; 15 con 6. Estas comparaciones incluyen a los caracteres genitales con menores CVs (10,11,15) y a los caracteres somáticos con mayores CVs (1 a 6 y 9) (Figs. 3 y 4, Tabla 1).

2. Analisis de Agrupamiento (AAG).—En las hembras (Fig. 9) todas las medidas somáticas se encuentran altamente correlacionadas ($r > 0.924$) y a un nivel menor ($r = 0.672$) con el carácter genital 10 (longitud de espermatecas). A este grupo se incorpora el formado por el núcleo 8-9 ($r = 0.794$) más el carácter 7 ($r = 0.506$), índices somáticos que se unen con las medidas a nivel $r = 0.394$.

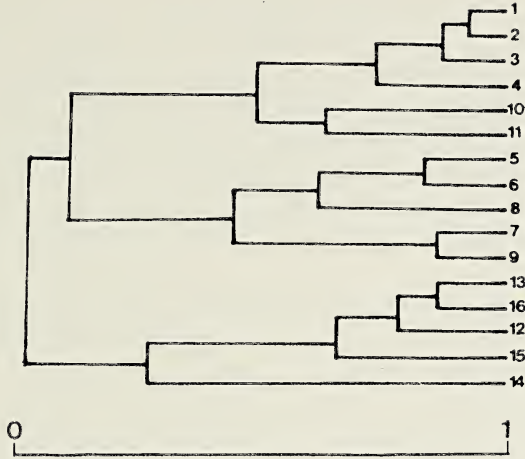
Se reconocen dos grupos más, formados por caracteres genitales y sus índices; el de los caracteres 12, 15, 13 que se une al cluster anterior a nivel $r = 0.156$ y el grupo de los caracteres 11, 14, 16 que se incorpora a nivel $r = 0.011$. Las correlaciones del carácter 10 con las medidas del cuerpo resultaron significativas al test Spearman ($p < 0.05$).

En los machos (Fig. 10) las medidas de patas (1-4) se unen a un nivel de correlación alto ($r > 0.729$). Este grupo se une a nivel $r = 0.490$ con el núcleo previo entre los caracteres genitales 10 y 11 ($r = 0.829$) que corresponden al largo y ancho basal del bulbo. Las correlaciones del carácter 10 con los caracteres 1, 5 y 6 (medidas) resultaron significativas al test Spearman ($p < 0.05$). Los caracteres 5 y 6 (largo y ancho de cefalotorax) se unen a un nivel alto de correlación ($r = 0.837$). Dicho núcleo se une a niveles más bajos con el carácter 8 ($r = 0.860$) y a nivel $r = 0.445$ con el núcleo 7-9 previamente unido ($r = 0.860$). Este grupo (caracteres 5-9) se une con el anterior a nivel $r = 0.104$.

Se reconoce un tercer grupo de caracteres (13, 16, 12, 15, 14) unido al cluster anterior a nivel $r = 0.019$.

DISCUSION

La uniformidad relativa de los caracteres genitales en algunas especies de arañas ha sido señalada en las revisiones sistemáticas de Blasco-Feliu (1986),



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Figura 10.-Fenograma de caracteres en machos de *G. mollicoma*, técnica R, 16 caracteres, $n = 24$, coeficiente de correlación, UPGMA.

Coyle (1968, 1971, 1974, 1985), G. de Pikelin y Schiapelli (1969), Schiapelli y G. de Pikelin (1962) y Vollrath (1980). Tales hechos han tenido consecuencias sobre la utilidad sistemática de los caracteres genitales como específicos de especie. Datos semejantes han sido utilizados para la reinterpretación de las hipótesis de selección sexual (Eberhard 1985). Particularmente en *Grammostola*, la variabilidad relativa de los caracteres genitales ha sido causa de controversia (Schiapelli y G. de Pikelin 1962a, b; G. de Pikelin y Schiapelli 1969; Bucherl 1951; Lucas y Bucherl 1965).

A diferencia de lo señalado por Schiapelli y G. de Pikelin (1962a, b) en *G. mollicoma* los caracteres genitales presentaron CVs mayores o iguales a los de los caracteres somáticos, particularmente en las hembras. Las hembras de *G. mollicoma* continúan mudando y creciendo después de la muda de maduración y es posible explicar la mayor variación de las dimensiones genitales de las hembras por mecanismos de crecimiento alométrico de las espermatecas. Datos tomados de seis mudas consecutivas de un individuo adulto de *Grammostola* sp. (Schiapelli y Gerschman 1962) indican un mayor crecimiento relativo de las espermatecas en relación al cefalotorax y patas I y IV. El crecimiento total de los caracteres somáticos en esas seis mudas fue: cefalotorax 27.08%, pata I 19.01%, pata IV 31.75%; mientras que los caracteres genitales (tomados de los dibujos de dichas autoras) se incrementaron así: 10: 40.69%, 11:66.57%, 12:24.89%, 13:19.88%. Al igual que en los resultados de la muestra estudiada, durante el crecimiento el carácter 13 (cuello mínimo de la espermateca) es el menos variable dentro de los genitales. La variación de los caracteres genitales en los machos es también mayor o igual a la de los somáticos. La variación de caracteres genitales fue mayor en las hembras que en los machos, lo que está de acuerdo con el estudio experimental. La variación de caracteres en machos probablemente esté determinada evolutivamente por la variación de genitalia en las hembras. No obstante no hay evidencia a favor de un mecanismo de aislamiento reproductor tipo llave-cerradura, dada la relativa simplicidad de estructuras. Los resultados podrían explicarse por las hipótesis de selección sexual por elección de la hembra,

como ha sido postulado por Eberhard (1983, 1985). Las cópulas observadas sugieren que un macho es capaz de copular con hembras que presentan espermatecas de morfología variable, lo que podría contraponerse a la hipótesis de selección sexual por elección de la hembra. No obstante, no hay pruebas definitivas sobre el éxito de tales cópulas (no se determinó si ocurrió inseminación y fertilización) por lo que la hipótesis de elección de la hembra mantiene su validez para explicar los resultados. Por otra parte, no puede descartarse una disminución en la selectividad de las hembras debido a las condiciones experimentales.

La selección sexual por elección de la hembra estaría condicionada en *G. mollicoma* por el tamaño de la hembra y de las espermatecas (correlacionados en el AAg). Para cada tamaño de hembra existiría un tamaño de bulbo a ser seleccionado, correspondiente a la óptima estimulación. Machos con bulbos pequeños pueden copular exitosamente con hembras pequeñas; estas hembras tienen una abundancia esperada mayor que las más grandes, de mayor edad. Machos con bulbos mayores pueden copular exitosamente con hembras más grandes, de abundancia esperada menor pero con mayor producción de huevos (Petersen 1950; Kessler 1973; Wise 1975, 1979: in Jocque 1983). Machos y hembras de tamaño intermedio tendrían posibilidades de encuentro y descendencia intermedias. De este modo las posibilidades de descendencia entre machos con bulbos de diferentes tamaños serían semejantes. La menor variación de caracteres genitales en los machos no contradice la hipótesis de elección de la hembra (Eberhard 1985:143). Esta diferencia de variación podría deberse también a la ausencia de mudas posteriores a la maduración en los machos.

Las proporciones corporales indudablemente tienen un papel importante en el éxito de la cópula dado el sistema de sujeción de la hembra por las apófisis tibiales del macho (e.g., Bucherl 1951). Machos pequeños no pueden sujetar y elevar hembras grandes sin adoptar posiciones riesgosas y machos grandes tienen dificultad para sujetar y elevar hembras pequeñas sin hacerles perder el equilibrio (Costa y Pérez-Miles en prep.). Estos hechos sugieren una primera selección por tamaño que actuaría en fases tempranas del cortejo y precópula. La correlación encontrada entre algunos caracteres del bulbo y somáticos indicaría una posible selección indirecta del tamaño del bulbo a través del tamaño del macho, relativa al tamaño de la hembra. En las hembras se encontró que los caracteres somáticos covarían más entre sí que con los genitales. Probablemente esto obedezca al crecimiento alométrico de las espermatecas. Otras correlaciones encontradas entre índices y algunas medidas podrían ser efectos laterales introducidos por los índices, como lo señala Atchley et al. (1976).

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**BIOLOGY OF *PEUCETIA VIRIDANS*
(ARANEAE, OXYOPIDAE) IN SOUTH CAROLINA,
WITH SPECIAL REFERENCE
TO PREDATION AND MATERNAL CARE**

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ABSTRACT

We studied the biology of the green lynx spider, *Peucetia viridans*, in South Carolina, with emphasis on the selection factors that maintain extended maternal care. Nocturnal predation on the clutch was greater than diurnal predation. *Chiracanthium inclusum* (Araneae, Clubionidae) was the primary predator of eggs and emerged spiderlings. After producing a fertile egg sac in the field, female *P. viridans* produced at least three fertile sacs in the laboratory. In the field, females produced a second egg sac if their first sac was lost early in the season. In contrast with other studies, spiderlings were unable to exit from about 74% of the egg sacs without the aid of the mother.

INTRODUCTION

Maternal care in spiders ranges from short-term guarding of egg sacs in solitary species to long-term communal care of young in social species. The most common form of maternal care is a brief guarding period after the spiderlings have emerged from the egg sac (Brach 1976). In most families, this gregariousness is short-lived and usually disappears after the first post-eclosion molt. At this time, maternal behavior often disappears, and conflicts between mother and young can result in spiderlings being eaten (Foelix 1982).

The green lynx spider, *Peucetia viridans* (Hentz), mates only once and guards its egg sac and young until spiderling dispersal. After mating, the female feeds for several weeks, and oviposits 25-600 eggs into an egg sac which she anchors to the vegetation with silk (Whitcomb et al. 1966). Spiderlings emerge from the egg sac as second instars and remain on or around the sacs until dispersal by ballooning.

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The purpose of this study was to examine the biology of *P. viridans*, with emphasis on the role of predation as a selection factor favoring extended maternal care.

MATERIALS AND METHODS

Study site.—The study site is located approximately 2.3 km SE of Clemson University in Clemson, Pickens County, South Carolina. The site consists primarily of grasses and forbs and is bordered on the east by Lake Hartwell and on the west by woody vegetation.

We made observations every day from 25 September through 20 December 1987 and once per week from 21 December through 18 January 1988 for approximately 2-4 h, starting at 1230 EST. In addition, nocturnal observations were made from 28 September through 13 October 1987 for 2-4 h, beginning at 2230 EST. By the latter date, predation ceased because of low nighttime temperatures. The study area was divided into four sections, and a different section was selected sequentially as the starting location each day. Additional field observations were made once per day from 4 September through 6 December 1988.

From 7 October 1987 through 20 May 1988 and from 9 September through 9 December 1988, we conducted laboratory studies in a rearing chamber maintained at $25 \pm 2^\circ\text{C}$ and $65 \pm 4\%$ relative humidity, with a 14L:10D photoperiod. In experiments lasting longer than 48 h, we fed each green lynx female one muscid fly three times per week.

Natural history observations.—*Laboratory studies:* To determine whether *P. viridans* females could produce more than one egg sac, we removed 46 females from their field sacs in 1987 and housed them individually in plastic containers (6.1 cm deep x 4.0 cm diameter) in the laboratory. We also removed females from sacs produced in the laboratory within one day after spiderlings emerged. For each egg sac, we recorded the date of construction, date of spiderling emergence, number of unhatched eggs, and number of spiderlings. When females died, we counted mature (chorionated) eggs in the ovaries. We recorded how many days spiderlings required to emerge from successive sacs and how many days females required for subsequent oviposition (empty sacs disregarded). To determine whether spiderlings could emerge from egg sacs without the aid of the mother, we removed 43 egg sacs from guarding females in September 1988 and housed the sacs in the laboratory. Sacs were not removed until 24 h after construction to allow time for the silk to harden. When females constructed second egg sacs in the field, we also removed these sacs 24 h after construction. If no spiderlings emerged from egg sacs within 65 days after construction, we opened the sacs to determine the fate of the clutch.

Field studies: In the field, we determined the percentage of guarding females occupying each species of plant ($N = 82$) and the height of the egg sacs above the ground ($N = 81$). Some females pulled leaves around the sacs, and tied the leaves together with silk, which formed shelters that hid the sacs from view. Using two treatments, sheltered sacs ($N = 19$) and unsheltered sacs ($N = 11$); we tested the null hypothesis that predation on egg sacs was independent of the presence of a shelter in *Rubus argutus* Link (blackberry), the primary plant used for egg-sac anchorage.

Prey items of females and spiderlings were recorded. Feeding rates of females and spiderlings were calculated by dividing the number of feeding observations on each group (gravid females, females after egg-sac loss, females guarding spiderlings, females guarding egg sacs, and unguarded spiderlings) by the total number of observation periods for each group.

Egg sacs consist of a flat disc attached to a round bowl. Using the bowl as a reference point, we determined the orientation of the egg sacs once every 24 h until the first spiderlings emerged. An orientation change was recorded when the bowl direction differed by one major compass subdivision (22.5°) or more from one observation period to the next. For each female, we calculated the percentage of observation periods during which orientation changed. These percentages were ranked and analyzed with analysis of variance to compare changes in bowl orientation in the absence of the female ($N = 25$) versus changes in orientation in the presence of the female ($N = 53$).

To determine whether females could produce a second egg sac in the field, we located 43 gravid females in September 1988 and tracked them until construction of the first sac, removed the first sac, and noted whether additional sacs were produced. To aid in identification of females, each female was given a unique mark on the abdomen or legs with orange, water-proof enamel.

Predation experiments.—*Field studies:* In the field, we randomly assigned each spider to one of three treatments. Each plant occupied by a female was marked with a numbered ribbon, and the coloration and markings of each female were recorded. In treatment 1, we removed females from their egg sacs on 25 September ($N = 26$). In treatment 2 ($N = 28$), we removed females from spiderlings after approximately 90% of the young had emerged from the egg sac. Treatment 3 served as a control ($N = 29$), with females left to guard both egg sacs and spiderlings. Mortality was only attributed to predation if we observed a predator consuming eggs or spiderlings or if dissection of the predator revealed eggs or young.

Over the course of the study, many of the samples fit the criteria of more than one treatment (e.g., disappearance of a guarding female would move the sample from treatment 3 to treatment 1). Because of this lack of independence between treatments, data were compared on a percentage basis. The total percentage of predation was calculated for unguarded egg sacs, unguarded spiderlings, guarded egg sacs, and guarded spiderlings. These percentages were calculated by dividing the total number of predators for each of the above four groups by the total number of observation periods for each group. When the same species of predator appeared on the same clutch in consecutive observation periods (observation periods began daily at 1230 EST and 2230 EST), it was counted only once. No predators were observed after 18 November, so observation periods beyond this point were not included in analyses.

Percentages of diurnal versus nocturnal predation were calculated for the four groups. Percentages of diurnal predation were calculated by dividing the total number of predators for each group by the total number of diurnal observation periods on that group. Percentages of nocturnal predators were calculated in a similar manner. Diurnal plus nocturnal predators do not always equal the total number of predators because if the same species of predator appeared on the same clutch in consecutive observation periods, it was recorded as a diurnal and a nocturnal predator. A 24-h absence was required between diurnal observations

and between nocturnal observations before counting the same species of predator on a particular clutch twice. Egg-sac and female disappearances were also recorded.

We deposited voucher specimens of *P. viridans*, predators, and prey items in the Clemson University Arthropod Collection.

RESULTS

Natural history observations.—*Laboratory studies:* The fertility (number of spiderlings plus number of unhatched eggs) of *P. viridans* decreased with consecutive egg sacs (Table 1). In the laboratory, a second egg sac was constructed by 93.5% of the females (16.3% of the sacs were empty), a third sac by 45.6% of the females (19.0% were empty), a fourth sac by 8.7% of the females (25.0% were empty), and a fifth sac (empty) by 2.2% of the females. Females did not open sacs without spiderlings ($N = 22$), whereas, females opened sacs with spiderlings ($N = 39$) except when the females died prematurely ($N = 4$). Spiderlings in these unguarded sacs were unable to emerge. At death, females ($N = 26$) contained an average of 11.7 ± 1.9 ($\bar{X} \pm \text{SE}$) mature eggs. Spiderling-emergence times from successive egg sacs were relatively constant (21-28 days). The amount of time required for oviposition decreased with successive sacs (Table 2).

Of the 43 egg sacs (second sacs excluded) taken into the laboratory in 1988, 27.9% of the sacs had spiderlings emerge without maternal aid. An average of 81.1 ± 22.4 spiderlings ($53.9 \pm 12.6\%$ of the total number of spiderlings in these sacs) emerged. Spiderlings made no exit holes in 27.9% of the sacs, whereas 62.8% of the sacs had one exit hole, and 9.3% of the sacs had two exit holes. Of the sacs with single exit holes, 29.6% had spiderlings lodged in the holes; 77.8% of spiderlings trapped in the holes failed to complete ecdysis. No spiderlings were lodged in the exit holes of sacs with two openings. Of the 6136 spiderlings trapped in the 43 egg sacs, 763 (12.4%) were trapped in their exuviae while trying to molt (Table 3). After 65 days, an average of 3.0 ± 1.3 live spiderlings was found in six of the egg sacs (range = 1-7 spiderlings/sac), and three of these sacs had exit holes.

Table 1.—Clutch sizes and spiderling emergence times from consecutive egg sacs constructed by *Peuceetia viridans* in 1987 and 1988. a = after spiderlings hatched, shed chorions were counted; sacs were not included in the analysis when spiderling number was greater than the number of shed chorions or when eggs were oviposited without the protection of an egg sac, b = sacs were constructed in the field; all others were constructed in the laboratory, c = sacs were constructed September-October 1988. (SE = standard error). NA = not applicable because spiderlings did not emerge from sacs.

	No. spiderlings ($\bar{X} \pm \text{SE}$)	N^a	No. unhatched eggs ($\bar{X} \pm \text{SE}$)	N	Emergence times (days) ($\bar{X} \pm \text{SE}$)	N
Sac #1 ^b	144.7 ± 10.04	34	5.7 ± 3.19	46	—	—
Sac #2	18.2 ± 2.19	42	5.6 ± 1.40	43	27.0 ± 0.28	31
Sac #3	11.6 ± 3.79	19	12.2 ± 3.24	20	27.8 ± 0.70	8
Sac #4	2.0 ± 2.00	4	7.2 ± 6.59	4	21.0	1
Sac #5	0.0	1	0.0	1	NA	0
Sac #1 ^{b,c}	165.3 ± 8.68	43	7.7 ± 10.98	43	24.8 ± 1.50	12
Sac #2 ^{b,c}	57.2 ± 33.28	4	52.2 ± 25.32	4	28.0	1

Table 2.—Interval between sequential ovipositions of *Peucetia viridans*. a = egg sacs were constructed in the field; all others were constructed in the laboratory, b = sacs were constructed in 1987, and females were allowed to guard until spiderlings emerged, c = sacs were constructed in 1988, d = value is a minimum, as determined from the first day each field sac was located. (SE = standard error).

	No. days between oviposition events ($\bar{X} \pm \text{SE}$)	N
Sac #1 ^{a,b} -Sac #2 ^b	73.8 \pm 7.84 ^d	9
Sac #2 ^b -Sac #3 ^b	45.8 \pm 2.05	16
Sac #3 ^b -Sac #4 ^b	40.0 \pm 3.46	3
Sac #1 ^{a,c} -Sac #2 ^{a,c}	27.2 \pm 2.50	4

Only two of the second egg sacs ($N = 4$) from 1988 contained spiderlings (two contained only eggs) (Table 1); 120 spiderlings (96.8% of the total) emerged from one sac, whereas all 105 spiderlings failed to emerge from the other sac despite the fact that this sac had three exit holes.

Field studies: Females used seventeen species of plants for oviposition (Willey 1988), with one female per plant. *Rubus argutus* ($N = 30$) and *Eupatorium hyssopifolium* L. ($N = 13$) predominated. The average egg-sac height was 73.8 ± 3.0 cm above ground (range = 21.5-161.5 cm), which represented the top 1/4 of all plants. When females constructed shelters, they placed their sacs inside the shelters and remained in direct physical contact with the sacs until spiderlings emerged; they then moved to the outside of the shelters to guard. Predation on the sacs was independent of the presence of *R. argutus* shelters ($\chi^2 = 0.151$, $df = 1$, $P = 0.6979$).

Adults fed on prey items in five insect orders, and spiderlings fed on insects in three orders and cannibalized conspecifics (Willey 1988). Hymenoptera ($N = 32$) were the primary prey of adult females. We observed 15 females feeding in the presence of spiderlings, but the females moved at least 3 cm away from the clutch and did not share the prey. We observed six spiderlings feeding on small insects; two fed simultaneously on the same ant. Gravid females had the highest feeding rate (10.6%), followed by females after egg-sac loss (6.2%), females guarding spiderlings (3.8%), unguarded spiderlings (1.2%), females guarding egg sacs (1.1%) and guarded spiderlings (0.0%).

Guarded egg sacs were reoriented significantly more often than unguarded sacs ($F = 56.70$, $df = 1$, $P = 0.0001$). Of the 53 guarding females, 51 reoriented their egg sacs an average of $67.7 \pm 2.8\%$ of the time; the remaining two sacs had spiderlings emerge on 28 September and 5 October, so reorientation may have occurred prior to initiation of the study. Of the 25 unguarded egg sacs, eight showed no reorientation, and the remaining 17 had orientation changes of $<$

Table 3.—Fate of *Peucetia viridans* spiderlings in unguarded egg sacs in 1988. a = calculated using total spiderling number, b = calculated using number of spiderlings trapped in egg sacs, c = egg sacs containing no spiderlings were omitted from analyses. (SE = standard error)

	N	None trapped in egg sacs ($\bar{X} \pm \text{SE}$)	% trapped in egg sacs ($\bar{X} \pm \text{SE}$) ^a	None trapped in exuviae ($\bar{X} \pm \text{SE}$)	% trapped in exuviae ($\bar{X} \pm \text{SE}$) ^b
Sac #1	43	142.7 \pm 11.24	84.9 \pm 5.06	17.7 \pm 4.49	12.4 \pm 2.80
Sac #2	2 ^c	54.5 \pm 50.50	51.6 \pm 48.38	0.0 \pm 0.00	0.0 \pm 0.00

22.5°; these changes were probably due to a gradual weakening of the silk attachment lines from wind and rain.

The earliest egg sac was constructed on 8 September 1988; in 1987, the first egg sac was located on 10 September. After losing their first egg sac, all 43 females relocated to different plants. We were able to find and follow only four of these females until they constructed second sacs. Oviposition into second egg sacs required less time in the field than in the laboratory (Table 2).

Predation experiments.—*Field studies:* Predation was greater when the female was absent (Table 4). The total percentage of predation was greatest for unguarded egg sacs (6.5%), followed by unguarded spiderlings (1.2%), guarded egg sacs (0.1%), and guarded spiderlings (0.0%).

Chiracanthium inclusum (Hentz) was the most frequently observed predator of unguarded egg sacs and spiderlings, and secondarily used the sac as a retreat. This predator commonly constructed a silk retreat against the egg-sac disc, chewed a hole through the disc, and fed on the clutch from the protection of its retreat. *Chiracanthium inclusum* was observed inside egg sacs where it presumably fed on the sac contents. This predator was seen only once in the presence of a guarding female, but was not observed feeding.

In contrast, we observed *Cesonia bilineata* (Hentz), a gnaphosid spider, remain undetected within a clutch of guarded spiderlings for 15 h. Although the predator was never observed eating spiderlings, it was surrounded by dead spiderlings and moved within the clutch until the guarding female approached, at which time it ceased movement until the female moved away.

The female also was unable to protect the clutch from ants when large numbers were present. We observed a colony of *Crematogaster* sp. swarm over a guarded egg sac. The female moved 6 cm from the egg sac while ants entered the sac and carried spiderlings away. Approximately 12 h later, the female relocated her egg sac. At this time, the egg sac contained two holes, and *Crematogaster* sp. were still detectable within the sac.

Unguarded clutches attacked by orthopterans and hymenopterans (with the exception of *Vespula* sp.) were completely destroyed. Orthopterans consumed entire clutches plus the sac in less than 30 min; ants carried away whole clutches overnight. In contrast, predators such as *C. inclusum*, *Cesonia bilineata*, and larvae of *Chauliognathus pennsylvanicus* (De Geer) (Coleoptera, Cantharidae) spent several days feeding on a clutch without consuming all of the eggs or young. Gaggrellids fed at sacs for less than 1 h and consumed from one to two eggs.

The percentage of nocturnal predation was greater than diurnal predation in all treatments but one (Table 5). Both diurnal and nocturnal predation were greater in the absence of the female. We observed 17 incidents of diurnal predation and 21 incidents of nocturnal predation (Table 4). *Chiracanthium inclusum* was the most common diurnal and nocturnal predator.

During the study, 15 unguarded egg sacs disappeared, presumably from rain, wind, or predation, and 10 sacs disappeared simultaneously with their guarding females, presumably because of relocation or predation. Nine egg sacs disappeared from guarding females, although the females remained. In six instances, guarding females disappeared from their egg sacs, presumably because of predation; the remaining clutches eventually disappeared or suffered mortality from predation.

Table 4.—Predators of *Peucetia viridans* clutches. a = total predation does not always equal diurnal plus nocturnal predation (see text).

	Number of predators		
	Diurnal	Nocturnal	Total ^a
UNGUARDED SACS			
Opiliones, Gagrellidae, undet.	—	3	3
Araneae			
<i>Chiracanthium inclusum</i> (Hentz)	3	6	8
Orthoptera			
<i>Campylacantha olivacea olivacea</i> Scudder	1	—	1
<i>Melanoplus</i> sp.	1	—	1
<i>Oecanthus</i> sp.	1	2	3
Coleoptera			
<i>Chauliognathus pennsylvanicus</i> (De Geer), larval stage	2	5	6
Hymenoptera			
<i>Crematogaster clara</i> Mayr	1	—	1
<i>Crematogaster minutissima</i> Mayr	—	1	1
<i>Crematogaster</i> sp.	1	1	1
<i>Paratrechina parvula</i> (Mayr)	—	1	1
UNGUARDED SPIDERLINGS			
Araneae			
<i>Chiracanthium inclusum</i>	2	1	3
<i>Cesonia bilineata</i> (Hentz)	1	—	1
Orthoptera			
<i>Campylacantha olivacea olivacea</i>	1	—	1
Hymenoptera			
<i>Paratrechina parvula</i>	1	—	1
<i>Vespa</i> sp.	1	—	1
GUARDED SACS			
Hymenoptera			
<i>Crematogaster</i> sp.	1	1	1

DISCUSSION

In South Carolina, the most frequent predator of *P. viridans* eggs was *C. inclusum*, followed by *Ch. pennsylvanicus* larvae, Orthoptera, and gagrellids. In northern Florida, Fink (1986, 1987) found that the two major sources of mortality of *P. viridans* egg sacs were ant predation, and parasitism by *Mantispa viridis* Walker (Neuroptera, Mantispidae); however, ants were the primary factor favoring maternal care of egg sacs because the female's presence did not significantly reduce mantispid parasitism. We did not observe mantispid parasitism in South Carolina and, although mantispids are common in the area,

Table 5.—Diurnal and nocturnal predation (%) on *Peucetia viridans* clutches (% = No. predators/No. observation periods). a = no. of observation periods.

	Diurnal predation (N) ^a	Nocturnal predation (N)
Unguarded sacs	3.8 (262)	13.8 (138)
Unguarded spiderlings	1.3 (470)	1.0 (98)
Guarded sacs	0.1 (865)	0.2 (577)
Guarded spiderlings	0.0 (325)	0.0 (65)

Brushwein (1986), in 4 years, located only two sacs that contained mantispids. In eastern Texas, mantispid parasitism did not constitute a significant source of mortality of *P. viridans* eggs (Killebrew 1982).

In South Carolina, the most frequent predator of emerged spiderlings was *C. inclusum*. In northern Florida, *C. inclusum* was observed in or on five unguarded egg sacs (10.9%), but Fink (1987) stated that *C. inclusum* was not observed feeding on eggs or spiderlings and might be using empty sacs only as a retreat. Fink (1986) concluded that in northern Florida, salticids were the major predators of emerged spiderlings; however, Fink (1986, 1987) made only diurnal observations, so nocturnal predators were not detected.

Although predation on egg sacs was independent of the presence of *R. argutus* shelters, this is the first report of *P. viridans* females constructing foliage shelters for their young. It is possible that the shelters protect the egg sacs from predation by making the sacs difficult to locate. Conversely, if a predator finds the sac, it may be protected while it forages. *Pisaurina* spp. and *Dolomedes* spp. (Araneae, Pisauridae) also construct shelters by pulling leaves over the sacs and tying them together with silk (Gertsch 1979).

Although females fed in the presence of spiderlings, we found no evidence that they directly provided food for the young, as reported by Whitcomb et al. (1966). However, spiderlings did feed on small insects that became trapped in the female's silk. We observed two cases of cannibalism among spiderlings in the field, whereas Fink (1984) did not observe any aggression among the young.

In the field, *P. viridans* females consistently reoriented their egg sacs throughout the guarding period. This behavior may regulate temperature of the sac contents and ensure that the eggs develop at the same rate. Randall (1977) found that the adaptive significance of maternal care in *P. viridans* was directly related to the female's role in reorienting the egg sac; when sacs were prevented from being reoriented, spiderlings emerged approximately four days late, which resulted in reduced clutch sizes because of cannibalism within the sacs.

Unguarded spiderlings failed to emerge from 74% of the egg sacs, and subsequently died within the sacs, suggesting that opening the sac might be an important component of maternal care in *P. viridans*; however, low laboratory humidity (65%) might have adversely affected the ability of spiderlings to emerge. In contrast, Randall (1977) and Fink (1986) found that spiderlings were able to emerge from unguarded sacs. Our 1987 results indicate that females need a cue from inside the egg sacs in order to open them, because guarded sacs with no spiderlings were never opened, and guarded sacs with spiderlings were always opened. Randall (1977) also found that females received cues from within the sacs when it was time for the spiderlings to emerge.

Laboratory females in South Carolina produced up to three fertile egg sacs after producing a fertile sac in the field, but clutch size decreased in successive sacs. This decline could be due to sperm depletion, decreased egg production, or an inadequate food supply. The latter is likely because second egg sacs produced in the field in 1988 had a clutch size approximately 2.5 times greater than second sacs produced in the laboratory. Over half of the South Carolina females were gravid at death, so, physiologically, it was possible to produce more eggs, although other factors might have been limiting. Whitcomb et al. (1966) reported that females in the laboratory in Arkansas constructed up to six egg sacs, and

that successive sacs contained fewer eggs. Fink (1984) also reported a decrease in egg number in second egg sacs in northern Florida.

In South Carolina, oviposition into second egg sacs in the laboratory occurred after a minimum of 74 days and oviposition into second egg sacs in the field occurred after an average of 27 days; the difference may reflect food availability. Spiderlings in the laboratory required approximately 27 days within the egg sacs prior to emergence. Therefore, unless the first egg sac was lost early in the season, low temperatures, decreased foliage for sac anchorage, scarcity of prey items, and female mortality would lower the probability of a second sac being successful. Whitcomb et al. (1966) reported that in the laboratory in Arkansas (20-24°C), females constructed second egg sacs one to two months after construction of the first sac. These authors, therefore, hypothesized that in Arkansas, *P. viridans* did not have time to produce a second sac before the first frost. Fink (1984) noted that in north Florida, females constructing second sacs would not live long enough to guard them successfully, and she (1986) presented a detailed discussion of the adaptive significance of guarding the first egg sac in northern Florida. Second egg sacs have been reported in the field in southern California (Turner 1979; Polis in Fink 1986) and southern Florida (Fink 1986). We suggest that production of successive egg sacs at higher latitudes, such as in northern South Carolina, is adaptive only when the original sac is lost early in the season.

In *P. viridans*, maternal care reduces clutch mortality from predation; however, our observations indicate that predation pressures in South Carolina differ from those in Florida, and that protection from nocturnal predation and possibly aiding the young in emergence from the egg sac are important factors influencing the retention of maternal care.

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A REVISION OF THE GENUS *HENTZIA* (ARANEAE, SALTICIDAE)

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ABSTRACT

The genus *Hentzia* belongs in the subfamily Dendryphantinae of the family Salticidae. It appears to be closely related to "*Beata*" *wickhami* and the genus *Anicius*. Twenty species are recognized in this revision, occurring from Nova Scotia and Quebec in the north to northern South America in the south. The genus ranges along the coastal areas of Mexico on both sides of the continent north to Arizona in the west and through central Texas to Minnesota. Six new species are described. These are *H. calypso* from Jamaica, *H. chekika* from Florida, the Bahamas and Cuba, *H. cubana* from Cuba, *H. pima* from Arizona, *H. whitcombi* from Guadeloupe, Puerto Rico and a few other Caribbean islands, and *H. zombia* from Hispaniola. The genera *Parahentzia* Bryant 1943, and *Maeviobeata* Caporiacco 1947, are here made junior synonyms of *Hentzia*. *Parahentzia insignita* Chickering 1946, is made a junior synonym of *Anoka parallela* Peckham and Peckham 1894. *Anoka peckhami* Cockerell 1893, and *Wala albovittata* Keyserling 1885, become junior synonyms of *Icius vittatus* Keyserling 1885. All of these are placed in the genus *Hentzia*. *Balmaceda peckhami* Bryant 1940 is found to be the female of *H. tibialis* Bryant 1940. The female paratype of *Hentzia tibialis* Bryant 1940, is found to be the female of *Hentzia chekika* n. sp. Finally *Wala noda* Chamberlin 1916, is transferred from *Hentzia* to *Corythalia*.

INTRODUCTION

The genus *Hentzia* is composed of somewhat elongate jumping spiders with a primarily circum-Caribbean distribution. The genus was erected by Marx (1883), with *Epiblemum palmarum* Hentz 1832 as the type species. *H. mitrata* was described by Hentz as an *Attus* in 1846, the Peckhams erected the genus *Anoka* for *H. vernalis* in 1893 and Cockerell described *Anoka peckhami* from Jamaica in the same year. Roewer (1954) listed 14 species in the genus, including *antillana* Bryant, *audax* Bryant, *fimbriata* (F. O. Pickard-Cambridge), *footei* (Petrunkévitch), *grenada* (Peckham and Peckham), *noda* (Chamberlin), *parallela* (Peckham and Peckham), *peckhami* (Cockerell), *poenitens* (Chamberlin), *squamata* (Petrunkévitch), *tibialis* Bryant, *vernalis* (Peckham and Peckham), *mitrata* (Hentz), and *palmarum* (Hentz). Of these, "*Hentzia*" *noda* was found during the current study not to belong to the genus at all, belonging instead to the genus *Corythalia*, and *H. peckhami* was discovered to be a junior synonym of *Icius vittatus* Keyserling (now *Hentzia vittata*). Examination of material in the collections of the Museum of Comparative Zoology, the American Museum of Natural History, the Florida State Collection of Arthropods, and the United States National Museum of Natural History, has produced a total of six undescribed species, four represented by both sexes and two only by the female. In addition, the two species of

Parahentzia were added to *Hentzia*, with *P. insignita* Chickering made a junior synonym of *Hentzia parallela*. This brings the total number of species to 20.

The affinities of the genus *Hentzia* are somewhat difficult to determine. The genus appears to be a member of the subfamily Dendryphantinae and resembles "*Beata*" *wickhami* (Peckham and Peckham) and *Anicius dolius* Chamberlin in genitalic structure. The former species probably does not belong to the genus *Beata*, where it was placed by Edwards (1980) or to *Icius*, in which it was originally placed (Peckham and Peckham 1894). Its proper placement will have to wait for future studies. The latter species is the type species for the genus *Anicius*. Assigning a sister genus for *Hentzia* is problematic, but "*Beata*" *wickhami* and *Anicius dolius* are reasonable approximations (see section on relationships of *Hentzia* for a more complete discussion). The most extreme member of the genus, *H. vernalis*, was at first thought to belong to a sister genus - *Anoka* (it is the type for this genus), but further analysis seems to lead to the conclusion that it was probably derived from *Hentzia footei* and is thus a valid member of *Hentzia*. The so-called *Parahentzia*, *H. mandibularis*, *H. parallela* and *H. vittata*, are at another extreme for the genus.

The distribution of species in the Caribbean is probably the result of island speciation, some active dispersal and recent accidental transport by man. The genus is probably relatively recent in origin and the ease with which the spiders are transported probably explains the present wide distributions of such species as *H. antillana* and *H. vittata* more than any other factor. Other species, such as *H. audax* and *H. squamata* are more localized and are probably endemic island productions.

The species in this genus are commonly found on shrubs or trees, such as willows, oaks, palmettoes, palms, and mangroves, and on commercial crops such as citrus, soybeans and cotton (personal observation and Whitcomb et al. 1963). Populations can be relatively dense, as they were on black mangroves near Cedar Key (Way Key), Levy Co., Florida, in 1975 (Richman 1977, 1982). Most species have adults present throughout the year, although this is not true in the northern part of the ranges of *H. palmarum* and *H. mitrata*.

Egg sacs are produced during much of the year in the tropical and subtropical parts of the distribution of the genus. In Florida egg sac records from captive specimens ranged from March to October (Richman 1977). The eggs are laid in a silken sac, within a resting sac of silk constructed by the female. Records for *H. palmarum* indicate that the average egg clutch size for this species is around 15 (specimens from near Cedar Key, Levy County, Florida).

METHODS

In the following species accounts, most are represented by 10 measurements for each sex. The following measurements were found to be of use: total length, carapace length, width and height, width of ocular region anteriorly and posteriorly, and length of ocular region from bases of anterior median eyes (AME) to posterior edges of posterior lateral eyes (PLE), and length and width of chelicerae. All measurements are in mm. The leg formula refers to the comparative length of each of the four pairs of walking legs. Thus a formula of 1234 indicates that the legs are ranked exactly in the order of anterior to

posterior placement, whereas 2134 would indicate that the second pair was the longest, followed by the first, third and fourth. The placement of the posterior median eyes (PME) in relation to the anterior lateral eyes (ALE) and the PLE is also noted in the descriptions.

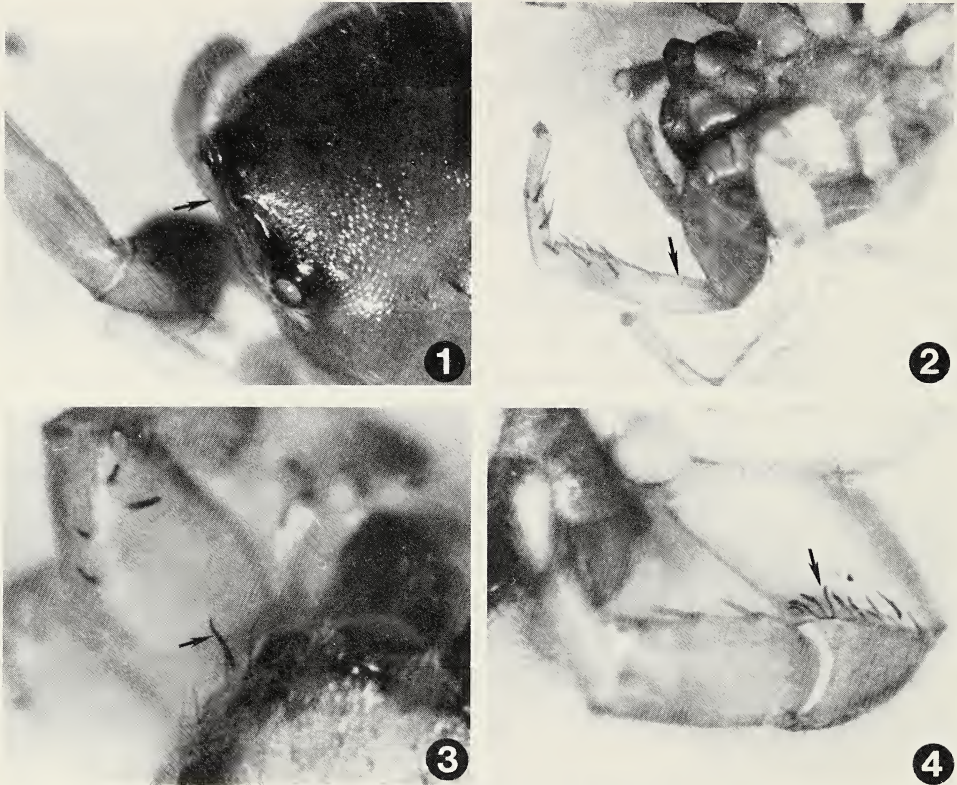
Sources for specimens examined are indicated by the following: Academy of Natural Sciences of Philadelphia (ANSP), American Museum of Natural History (AMNH), British Museum (Natural History) (BMNH), Bruce Cutler Collection (BC), Canadian National Collection (CNC), David B. Richman Collection (DBR), Exline-Peck Collection (now at the California Academy of Sciences) (EPC), Florida State Collection of Arthropods (FSCA), Museum of Comparative Zoology (MCZ), Texas A. & M. University (TAM), United States National Museum of Natural History (Smithsonian Institution) (USNMNH), University of California, Berkeley (UCB), and Universidad de Costa Rica (UCR).

The maps show the ranges of the twenty species, based on locality records that could be found on current maps. Some records were found that I could not place on the maps. This is especially true of records from Cuba and the Bahamas. For example, in a recent atlas of Cuba (Atlas Nacional de Cuba 1970) at least three listings are found for "Soledad", none of which match the locality for the specimens labeled "Soledad, Cuba." This locality is really part of the modern city of Cienfuegos. Other localities are more obscure. Many of the smaller Bahama Islands are also difficult to find on a map. I have, however, listed all locality records in the descriptive section, whether I could locate them on a map or not.

RELATIONSHIPS OF *HENTZIA*

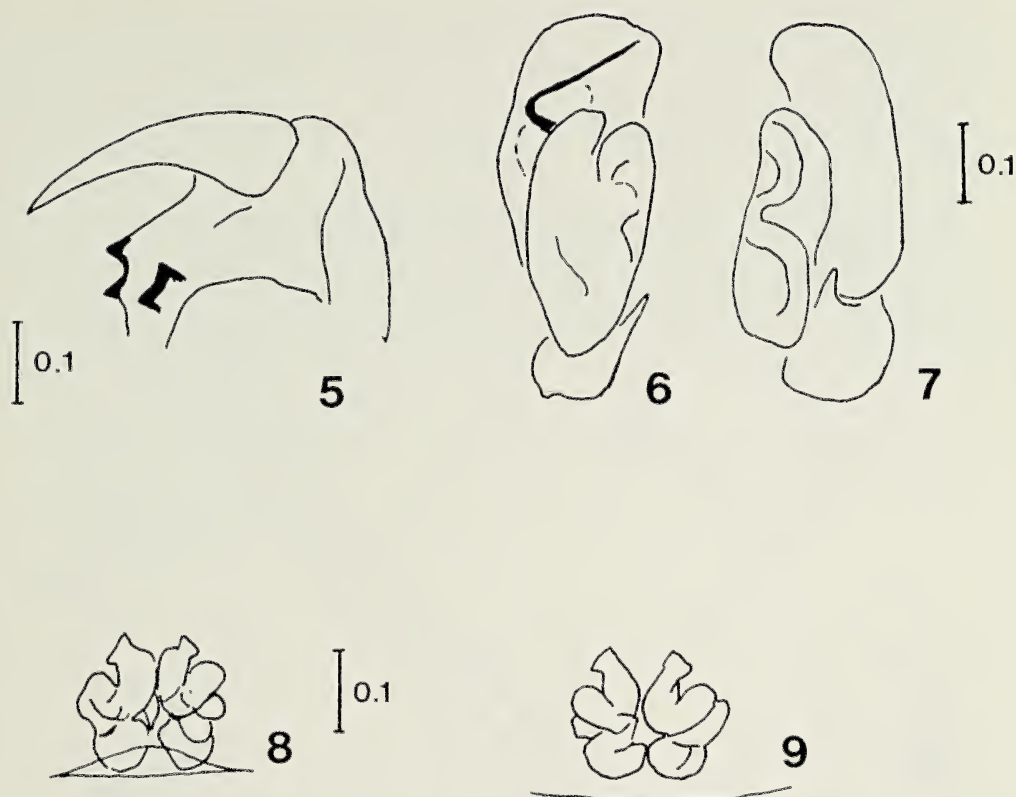
The genus *Hentzia* is here defined by the presence of *both* pencils of hair below the posterior median eyes and spatulate hairs on the ventral retromargin of the first patella and distal femur (Figs. 3, 4). These characteristics are most pronounced in the female, especially in regard to the hair pencils. Males often have elongated chelicerae and somewhat elongate bodies. The male palpi of most species exhibit a two-lobed bulb and a thin, curved embolus. This characteristic is shared with "*Beata*" *wickhami*. Males of *Hentzia* usually have simple or truncated retromarginal cheliceral teeth, whereas females have bicuspid retromarginal teeth.

As noted earlier, the genus *Hentzia* appears to be most closely related to "*Beata*" *wickhami* and *Anicius dolius*. Both species lack the hair pencils and spatulate hairs found in the females of *Hentzia* (Figs. 1-4) and also differ in the males having bicuspid (or bifurcate) retromarginal teeth (Figs. 5, 10). The retromarginal tooth of the male of *A. dolius* is barely bicuspid, however (Fig. 10). It is doubtful that *B. wickhami*, which was described in the catch-all genus *Icius*, really belongs in *Beata*. Its similarity to *Hentzia* in the structure of the palpus (Figs. 6, 7) is very striking. The female epigynum (Figs. 8, 9) is also quite similar. The male of *Anicius dolius* has a palpus that is different from that of *Hentzia*, but still the embolus is long and thin and generally similar to at least some of the *Hentzia* species (Figs. 11, 12). The female genitalia (Figs. 13, 14) also resemble that of some *Hentzia* species. Both sexes of *A. dolius* are close to *Hentzia* in general appearance. "*Beata*" *wickhami* is known from southern Florida, Cuba and the Bahamas. *Anicius dolius* and an apparent undescribed species of the same genus are from southern Mexico.



Figures 1-4.—Anatomical structures of *Anicius dolius* and *Hentzia*: 1, carapace of female *A. dolius*, showing lack of hair pencils; 2, ventral view of female *A. dolius*, showing lack of spatulate hairs on posterior ventral edge of femur and patella I; 3, carapace of *Hentzia antillana*, showing hair pencils below posterior median eyes; 4, ventral view of first leg of *Hentzia antillana*, showing spatulate hairs on femur and patella.

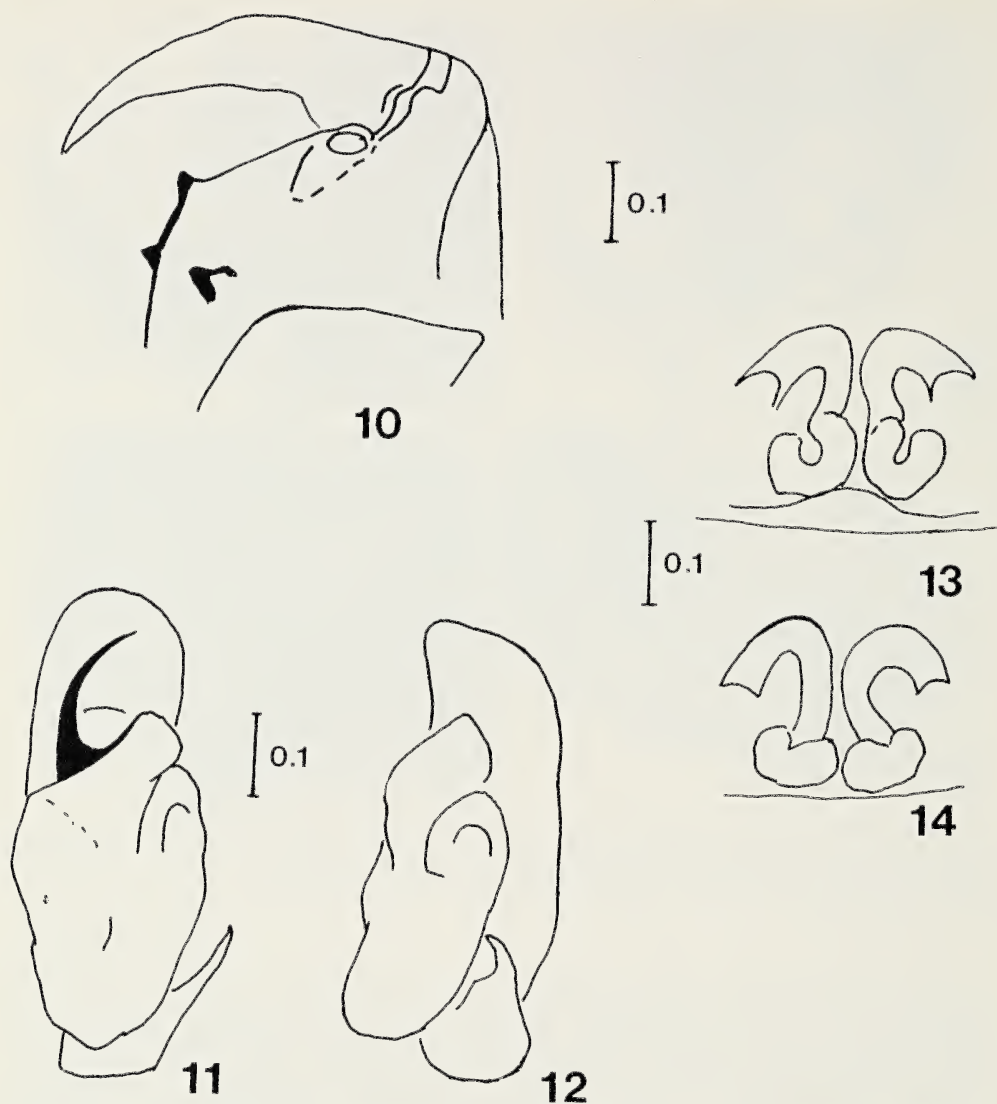
A cladogram (Fig. 15) shows the apparent relationships of "*B.*" *wickhami* and *A. dolius*, taken as a group, and the species groups of the genus *Hentzia*. Resolutions of species relationships within a group are based on characters not shown on the cladogram but are discussed in the text. For example, the two species *H. chekika* and *H. poenitans* have very similar epigynal structure, with the j-shaped tubes much shorter than in the next closest species *H. grenada*. They also lack the sperm tube loop found on the bulb of *H. grenada* male palpi. They are thus placed closer to each other than to *H. grenada* on the cladogram. Similarly, *H. audax* and *H. cubana* appear to be more closely related to each other than to the other members of the *palmarum* species group because the male chelicerae are nearly identical in location of teeth and both have male palpi with a hooked tibial apophysis. The males of this species are so similar, except in size, that for a long time I considered them to be just size variants of the same taxon. The females are, however, quite different in their epigynal structure. On the other hand, the relationships of the *vittata* group are not resolved, and many of the relationships within the *palmarum* group remains uncertain. I thus thought it best not to use more than the seven characters to separate the species groups for the cladistic analysis.



Figures 5-9.—*Beata wickhami* (Peckham and Peckham): 5-7, male from Habana, Cuba; 5, left chelicera, ventral view, showing bicuspid retromarginal tooth; 6, 7, palp; 6, ventral view; 7, retrolateral view; 8, 9, epigynum of female from Bahamas, 8, ventral view; 9, dorsal view.

The characters used in the cladogram are: 1) presence or absence of female hair pencils, 2) presence or absence of female spatulate hairs, 3) male retromarginal tooth type (bifurcate or bicuspid, simple, truncate [it should be noted that *H. footei* occasionally exhibits a bifurcate retromarginal tooth, but as the tooth is usually just truncate, the latter character was used in the analysis]), 4) male bulb shape (lobes equal, prolateral reduced), 5) female epigynum (with central cone-like structure, without central cone-like structure), 6) male promarginal teeth (equal, not equal), 7) female epigynal tubes (j-shaped, other). The weights and consistency index (c.i.) are represented on the legend of the cladogram. There are apparently four species groups in *Hentzia*, based on this analysis. These are: the *palmarum* group, the *grenada* group, the *vernalis* group and the *vittata* group. The *grenada* group and the *palmarum* group are perhaps the most closely related, based on the structure of the male palpi and chelicerae, but differ strongly in the structure of the female epigynum.

It should be noted that as this is a first attempt to construct a cladogram for *Hentzia*, the relationships should not be considered as proven. Because of the uncertainty involved in this cladogram and the lack of separation between species, there is no doubt in my mind that a better one can be, and probably will be, produced in the future. This can be considered as only a preliminary attempt.

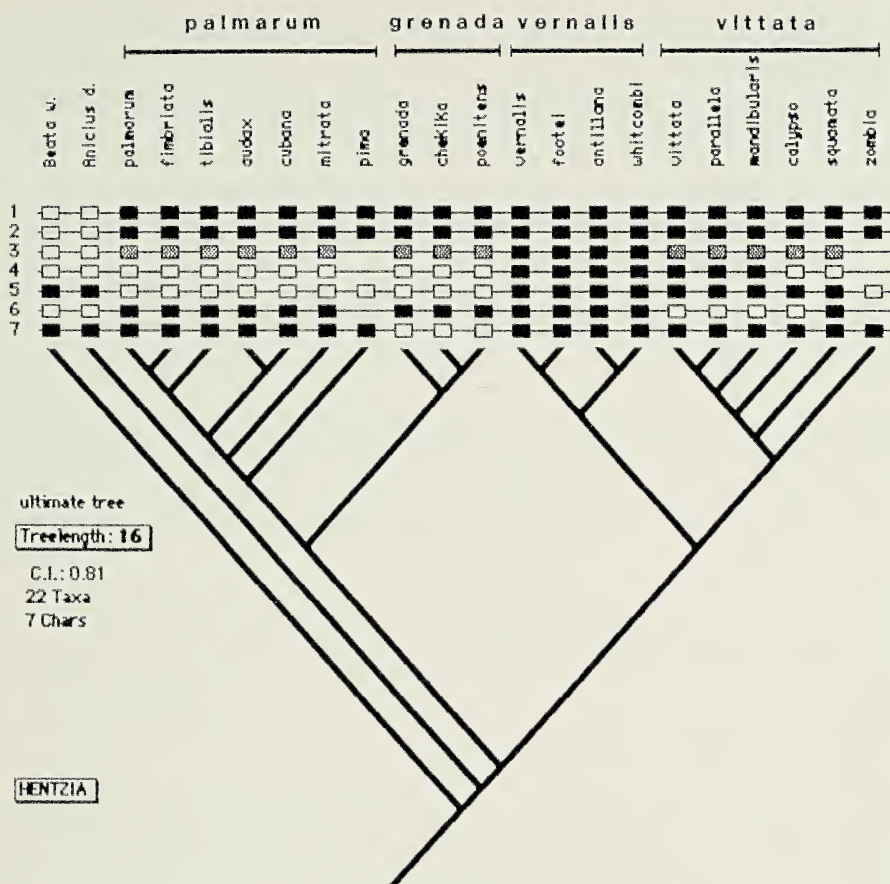


Figures 10-14.—*Anicius dolius* Chamberlin: 10, left chelicera of male from Michoacan, Mexico, ventral view; 11, 12, palp of holotype male from Guadalajara, Mexico; 11, ventral view; 12, retrolateral view; 13, 14, epigynum of female from Michoacan, Mexico; 13, ventral view; 14, dorsal view.

KEY TO THE SPECIES OF *HENTZIA*

Note: Any specimen found north of southern Georgia and east of a line from Minnesota south to west Texas is almost certainly either *H. palmarum* or *H. mitrata*. From southern Georgia through Florida *H. grenada* is also possible and *H. chekika* may be encountered in southern Florida.

1. Males 2
 Females 19
2. Tibial apophysis sinuate (Fig. 92); with 2-3 apparent retromarginal teeth (actually only one truncate retromarginal tooth on distal 1/4) (Figs. 89, 90); basal part of embolus reduced and more firmly attached to the



Character	type	weight	states	steps	C.I.
1. F hair pencils	r	2	2	1	1.00
2. F spatulate hairs	r	3	2	1	1.00
3. M retrotooth	u	2	3	2	1.00
4. M bulb	r	1	2	2	0.50
5. F epigynum	r	1	2	2	0.50
6. M prolegs	r	1	2	2	0.50
7. F epigtubes	r	1	2	1	1.00

1. F hair pencils: absent; present;
2. F spatulate hairs: absent; present;
3. M retrotooth: bifurcate; simple; truncate;
4. M bulb: lobes equal; prolateral reduced;
5. F epigynum: with cone; without cone;
6. M prolegs: equal; not equal;
7. F epigtubes: j-shaped; other;

Figure 15.—Cladogram of the genus *Hentzia*, based on seven morphological characters. Only species groups are separated by the characters used on the cladogram. Species separations are based on characters defined in the species group descriptions in the text. The four species groups defined are 1) *palmarum*, 2) *grenada*, 3) *vernal*, and 4) *vittata*. See text section on the relationships of *Hentzia* for discussion of characters used.

- tegulum (Fig. 91) (northern South America, St. Vincent, Trinidad and Barbados) *vernalis*
- Tibial apophysis curved, truncate or straight, never sinuate; always with one retromarginal tooth; embolus not reduced 3
3. Retromarginal tooth straight or curved and truncate or rarely bifurcate (Figs. 96, 97, 104, 109) 4
- Retromarginal tooth simple 6
4. Fang with at least one tooth (Figs. 96, 97) (Dominica, St. Lucia) *footei*
- Fang without teeth 5
5. Distal promarginal tooth equidistant from proximal promarginal and retromarginal tooth as seen from below (Fig. 109) (northern Lesser Antilles and Puerto Rico) *whitcombi*
- Distal promarginal tooth closer to retromarginal tooth (Fig. 104) (Cuba to St. Lucia) *antillana*
6. Tibial apophysis of palpus truncated and slanted (Fig. 47) (Cuba) *tibialis*
- Tibial apophysis usually spike-like or curved 7
7. Tibial apophysis distinctly curved (Cuba) 8
- Tibial apophysis straight or nearly so 9
8. Larger than 5.25 mm found only in the mountains of southeastern Cuba *audax*
- Never larger than 5.25 mm; usually 3-4 mm; widespread in Cuba *cubana*
9. Chelicerae covered with white scales (Fig. 146) (Mona Island, Puerto Rico) *squamata*
- Chelicerae not covered with white scales 10
10. First legs without pigment (Fig. 29); chelicerae rarely elongate; bulb noticeably expanded distally (Fig. 33) (Quebec south to Florida and west to Kansas, Oklahoma and Texas) *mitrata*
- First legs pigmented 11
11. Chelicerae robust in larger males, being nearly as wide as long 12
- Chelicerae elongate in larger males, much longer than wide 15
12. Chelicerae with dorsal tubercle (rarely absent) (Fig. 140) (Hispaniola) *mandibularis*
- Chelicerae without dorsal tubercle 13
13. Tiny species (ca. 3 mm) with distinctive dorsal abdominal markings (Fig. 130) (Jamaica) *calypso*
- Larger species (>3 mm), without distinctive dorsal markings (males difficult to distinguish) 14

14. Range from Panama along South American coast to Trinidad and Guyana*parallela*
Range Jamaica, Hispaniola, Cuba and the Bahamas*vittata*
15. Bulb with distinctive sperm duct loop (Figs. 70, 71); elongated species (Fig. 67) associated with small palms and cycads (Florida, Georgia)*grenada*
Bulb without sperm duct loop; sperm duct only slightly curved16
16. Dorsal abdominal pattern with 8-10 dark spots (Figs. 80, 81); associated with tall palm trees such as *Cocos* (Florida, Bahamas, Cuba)*chekika*
Pattern without 8-10 dark spots; not associated with tall palms17
17. Retromarginal cheliceral tooth opposite or nearly opposite proximal promarginal tooth (Figs. 18, 19) (Nova Scotia, east to Bermuda, south to Cuba, west to Oklahoma and Texas, northeastern Mexico)*palmarum*
Cheliceral teeth approximately equidistant (Figs. 37, 75)18
18. Anterior bulb lobe slanted and smaller than posterior (Fig. 76); relatively tiny species (ca. 3 mm) known only from Sonora*poenitens*
Anterior bulb lobe not slanted; lobes approximately equal in size; larger species (usually > 4 mm) (Tamaulipas south to Costa Rica, north along the Pacific coast to Nayarit)*fimbriata*
19. Covered with pink iridescent scales; epigynum with internal "cloverleaf" structure (Fig. 155) (Hispaniola)*zombia*
Without pink iridescent scales; epigynum not as in Fig. 15520
20. Epigynum as in Figs. 65, 66, with c-shaped openings; dorsal abdominal spot pattern block-like (Fig. 64) (Arizona)*pima*
Epigynum unlike Figs. 65, 66, with openings not c-shaped21
21. Tiny species (ca. 3-4 mm); dorsal abdominal pattern distinctive (Fig. 131); epigynum with large round openings less than one diameter apart (Figs. 135, 136) (Jamaica)*calypso*
Larger species (usually > 4 mm); epigynum with relatively smaller openings or openings not round22
22. Legs unpigmented; epigynum with long central tubular structure (Fig. 35) (Southern Canada south to Florida and west to Texas)*mitrata*
Legs pigmented; epigynum with short, bell-like, or no central structure23
23. With short bell-like structure on epigynum; epigynal openings rounded or forming atrium (Figs. 24, 26) (Nova Scotia to Bermuda and Cuba, west to Texas and northeastern Mexico) *palmarum*
With vague bell-like structure on epigynum, or with none; openings variable, but not as in *palmarum*24
24. Epigynum as in Figs. 93, 94, with apparent double lateral tubes in dorsal view; dorsal abdominal pattern lacking (Northern South America, Trinidad, St. Vincent, Barbados)*vernalis*

- Epigynum unlike Figs. 93, 94, with only one pair of tubes; with or without dorsal abdominal pattern25
25. Epigynum with trumpet-shaped openings (Figs. 107, 152)26
Epigynum otherwise27
26. Spermathecae larger in area than trumpet-shaped part of epigynum (Figs. 152, 153) (found only on Mona Island)*squamata*
Spermathecae equal in area to trumpet-shaped part (Figs. 107, 108) (Cuba, Hispaniola and Puerto Rico to St. Lucia)*antillana*
27. Epigynal openings circular or oval28
Epigynal openings not circular or oval30
28. With vague central bell-shaped structure on epigynum (Fig. 112) (Puerto Rico to Guadeloupe)*whitcombi*
Without vague bell-shaped structure29
29. Epigynal openings circular (Fig. 144) (Hispaniola)*mandibularis*
Epigynal openings oval (Fig. 128) (Central America, northern South America, east to Trinidad)*parallela*
30. Epigynum with characteristic "hump" anteriorly (Figs. 40, 42) (Tamaulipas south to Costa Rica and north to Nayarit)*fimbriata*
Epigynum not so constructed31
31. Epigynum wider than long32
Epigynum longer than wide34
32. Epigynum with complicated series of tubes (Fig. 51)*tibialis*
Epigynum relatively simple internally33
33. Abdomen lacking dorsal pattern (Fig. 74); small species - ca. 3 mm; found in Sonora, Mexico*poenitens*
Abdomen with distinctive pattern of five pairs of brown spots (Fig. 81); larger species - 5-6 mm; found in Cuba, the Bahamas and Florida...*chekika*
34. Epigynum with funnel-like or angulate openings (Cuba)35
Epigynum without funnel-like openings36
35. Epigynum with straight, trumpet-like tubes, leading to slit-like openings (Figs. 57, 58); large species (5.25 mm or larger) found in southeastern mountains of Cuba*audax*
Epigynum with tubes twisted laterally; openings oval; small species (usually 3-4 mm); widespread in Cuba; epigynum diagnostic (Figs. 62, 63) *cubana*
36. Epigynum with elongate tube leading to slit-like openings (Fig. 72) (Florida and southern Georgia)*grenada*
Epigynum with bent tube leading to openings37

37. Epigynal openings slanting posteriorly (Fig. 100) (Dominica to St. Lucia)*footei*
 Epigynal openings not slanting posteriorly, but laterally (Jamaica through Hispaniola and Cuba to the Bahamas)*vittata*

SPECIES ACCOUNTS

Hentzia Marx 1883

Attus Walckenaer 1805 (applied to nearly all salticids - junior synonym of *Salticus* Latreille 1804).

Epiblemum Hentz 1832 (applied to *Salticus* as well as *Hentzia*).

Hentzia Marx 1883, type species *palmarum* (Hentz) 1832.

Wala Keyserling 1885, type species *palmarum* (Hentz) 1832. Synonymy Bryant 1940.

Anoka Peckham and Peckham 1893, type species *vernalis* Peckham and Peckham 1893. Synonymy Bryant 1940.

Parahentzia Bryant 1943, type species *mandibularis* Bryant 1943. NEW SYNONYMY.

Maeviobeata Caporiacco 1947, type species *charitonovi* Caporiacco 1947. NEW SYNONYMY.

As noted in an earlier section, this genus is characterized by the primarily female characters of hair pencils below the PME and spatulate hairs on the ventral retromargin of the first patella and distal femur. Members of the genus are also characterized by males having long, thin emboli arising on the prolateral side of the tegulum and an anterior separation on the bulb, forming two lobes. *Hentzia vernalis* is an exception to the latter character, having the bulb partially reduced. Most males have elongate chelicerae and the first legs considerably darker than posterior three pairs. Females usually have spermathecae with a series of spiral twists and always have chelicerae with two simple promarginal teeth and one bicuspid retromarginal tooth. The retromarginal teeth of the male chelicerae are usually simple or truncate, the latter form often being bent distally.

SPECIES MISPLACED IN THE GENUS *HENTZIA*

Wala noda Chamberlin 1916 = *Corythalia noda* (Chamberlin), NEW COMBINATION. Holotype and paratype females from Torontoy, PERU, and female from Conservidayo River, PERU (MCZ) examined.

PALMARUM SPECIES GROUP

The *palmarum* species group consists of seven species of slightly elongate spiders with short to moderately elongate chelicerae and a bell-shaped or tubular central structure on the epigynum of the females. With the exception of *H. mitrata*, all of the known males have darkly pigmented or marked legs. The group is the most widespread of the species groups of *Hentzia*, being found from Nova Scotia to Bermuda, south to Cuba and South America, west to Oklahoma and Texas and north along the west Mexican coast as far as Nayarit and Sinaloa. One species, *H. pima* n. sp., is known from only one female, but appears to be a member of this group and occurs in southern Arizona.

At present, the species within this group and within the *vittata* group are perhaps the most difficult to relate by synapomorphic characters. In the case of

the *palmarum* group this is, at least in part, because several of the species are from Cuba and relatively little material is available. It appears that *H. palmarum*, *H. fimbriata* and *H. tibialis* are closely related, based on similarities in the structure of the palpi, such as the long, relatively thin and slightly curved tibial apophysis. It could be equally argued that *H. mitrata* would fit here as well, and I have left it next to *H. palmarum* in the species descriptions for convenience, but it differs from all the other species in the group in having long, white-fringed front legs and thus appears on the cladogram as a separate line (Fig. 15). Both *H. audax* and *H. cubana* have extremely similar males, except for size and thickness of the palpal tibial apophysis, but the females differ significantly (see species descriptions). Finally the male of *H. pima* is unknown and its placement on the cladogram is problematic. Until more material becomes available, especially from Cuba, the relationships of the species within the *palmarum* species group can only be assigned provisionally.

Hentzia palmarum (Hentz)

Figs. 16-28, Map 1

Epiblemum palmarum Hentz 1832:108 (type lost); 1846:366; Peckham and Peckham 1883:28.

Attus marginatus Walckenaer 1837:466 (type lost) (see Maddison 1986:142, 143).

Attus ambiguus Walckenaer 1837:467 (type lost); Chamberlin and Ivie 1944:201.

Hentzia palmarum Marx 1883:26; Kaston 1948:491; Chickering 1944:161.

Icius palmarum Peckham and Peckham 1888:46; Emerton 1891:232; Emerton 1902:56.

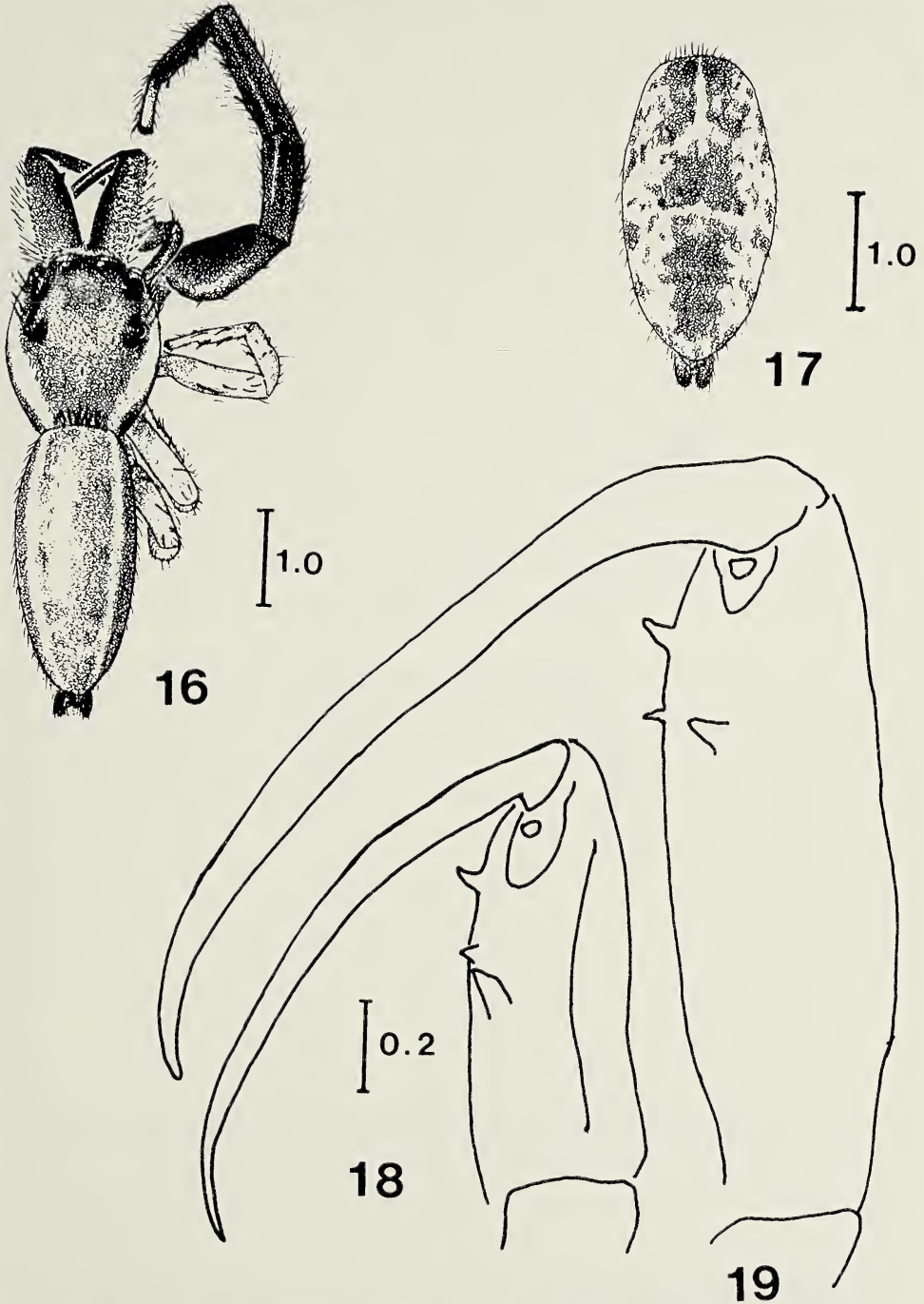
Anoka palmarum Peckham and Peckham 1894:126; Simon 1901:614.

Wala palmarum Peckham and Peckham 1909:508; Comstock 1912.

NOTE: *Icius vittatus* Keyserling 1885 and *Wala albovittata* Keyserling 1885 were incorrectly assigned as synonyms of *H. palmarum* and are instead senior synonyms of *Hentzia peckhami* (Cockerell).

Diagnosis.—Chelicerae of male with retromarginal tooth usually directly in line with proximal promarginal tooth (Figs. 18, 19) (separates this species from all but *H. mitrata*), bulb of male palpus with edges of distal half parallel or expanded (Figs. 20, 22), first legs pigmented (Fig. 16) (separates this species from *H. mitrata*), female epigynum with bell-like median structure (Figs. 24, 26). Chelicerae of male usually elongate; male chelicerae and first legs pigmented; median dorsal marking on posterior 1/3 of carapace if present thin (willow leaf shape); female often with herring-bone pattern; bodies of both male and female distinctly less elongate than those of *H. grenada* or *H. chekika* n. sp.

Male.—Total length 4.00-5.30. Carapace 1.60-2.00 long, 1.30-1.70 wide, 0.80-1.00 high at PLE. Ocular area 0.70-0.90 long, 1.00-1.30 wide anteriorly, 1.10-1.40 posteriorly. Chelicerae 0.75-1.80 long 0.30-0.45 wide (10 males from Cedar Key Levy Co., Florida). Carapace length and cheliceral length measurements (124 specimens from The Bahamas, Florida, Pennsylvania, Texas, Bermuda, Georgia, New Jersey, Ontario, Nova Scotia, North Carolina, South Carolina, Arkansas, Missouri, Massachusetts and Michigan, not including above specimens) 1.36-2.35 and 0.40-2.20 (Fig. 28). PME equidistant to ALE and PLE. Leg formula 1423. Carapace red to orange-brown with white scales forming willow-leaf marking on dorsal posterior 2/3 and lateral bands. Margin of carapace black, with dark area becoming wider toward posterior. Clypeus covered with white hairs. Eyes ringed with black except AME which are ringed with dark brown. Chelicerae dark red brown with pale promarginal 1/3. Labium dark brown with pale tip. Sternum



Figures 16-19.—*Hentzia palmarum* (Hentz): 16, male from Plymouth Co., Mass., dorsal view; 17, female from Highlands Co., Fla., dorsal view of abdomen; 18, left chelicera of male from Tulsa Co., Okla., ventral view; 19, left chelicera of male from Levy Co., Fla., ventral view.

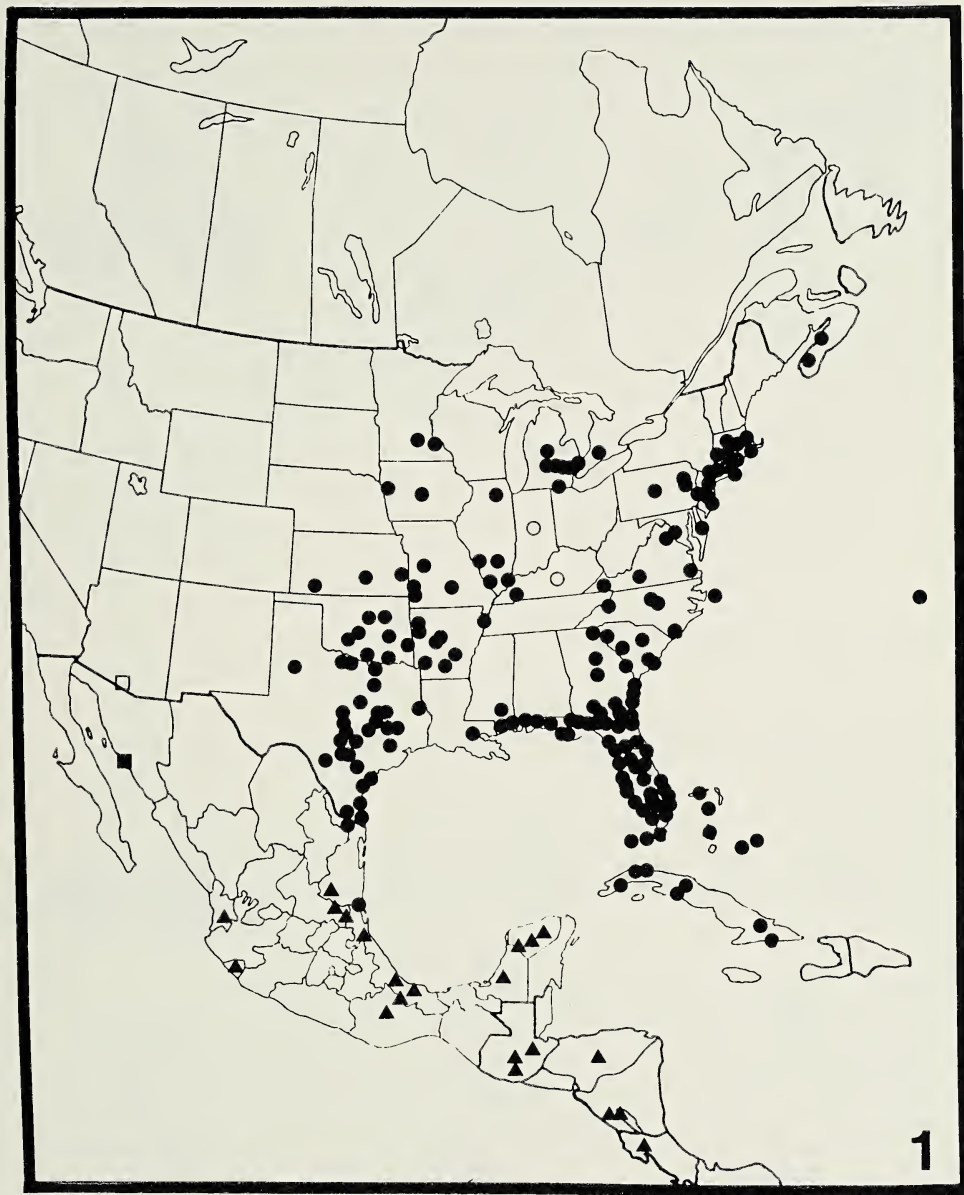
orange. Abdomen either with central dark band, lateral white scale bands on either side and venter brown or with 3-4 dark spots on the central band. Abdomen covered with iridescent scales. First leg red-brown, tarsus yellow, proximal metatarsus yellow, dorsal femur lighter brown. Other legs yellow. Palpi red-brown, cymbium yellow.

Female.—Total length 4.70-6.10. Carapace 1.90-2.40 long, 1.40-2.05 wide, 0.70-1.00 high at PLE. Ocular area 0.80-1.00 long, 1.20-1.45 mm wide anteriorly, 1.30-1.70 mm wide posteriorly. Chelicerae 0.50-0.80 long, 0.35-0.55 wide (10 females from Cedar Key, Levy Co., Florida). PME slightly closer to ALE than to PLE. Leg formula 1423. Carapace red-brown with lighter center which ends before posterior margin. Eyes ringed with black except AME ringed with brown. Carapace covered with white scales. Clypeus covered with white hairs. Chelicerae red-brown. Endites dark brown, prolateral 1/3 lighter. Labium dark brown with pale tip. Sternum orange-brown. Abdomen yellowish with dark central pattern, sometimes with herring-bone pattern or with three to four brown spots, similar to pattern of female *H. mitrata*. Front legs orange-brown with femur darker anteroventrally and patella and tibia darker distally. Other legs yellow. Palpi yellow with dorsal dark spots on proximal patella, tibia and tarsus.

Distribution.—Nova Scotia and Ontario south to Cuba and the Bahamas, east to Bermuda and west to Minnesota, Nebraska, Texas and Tamaulipas, Mexico. (Map 1).

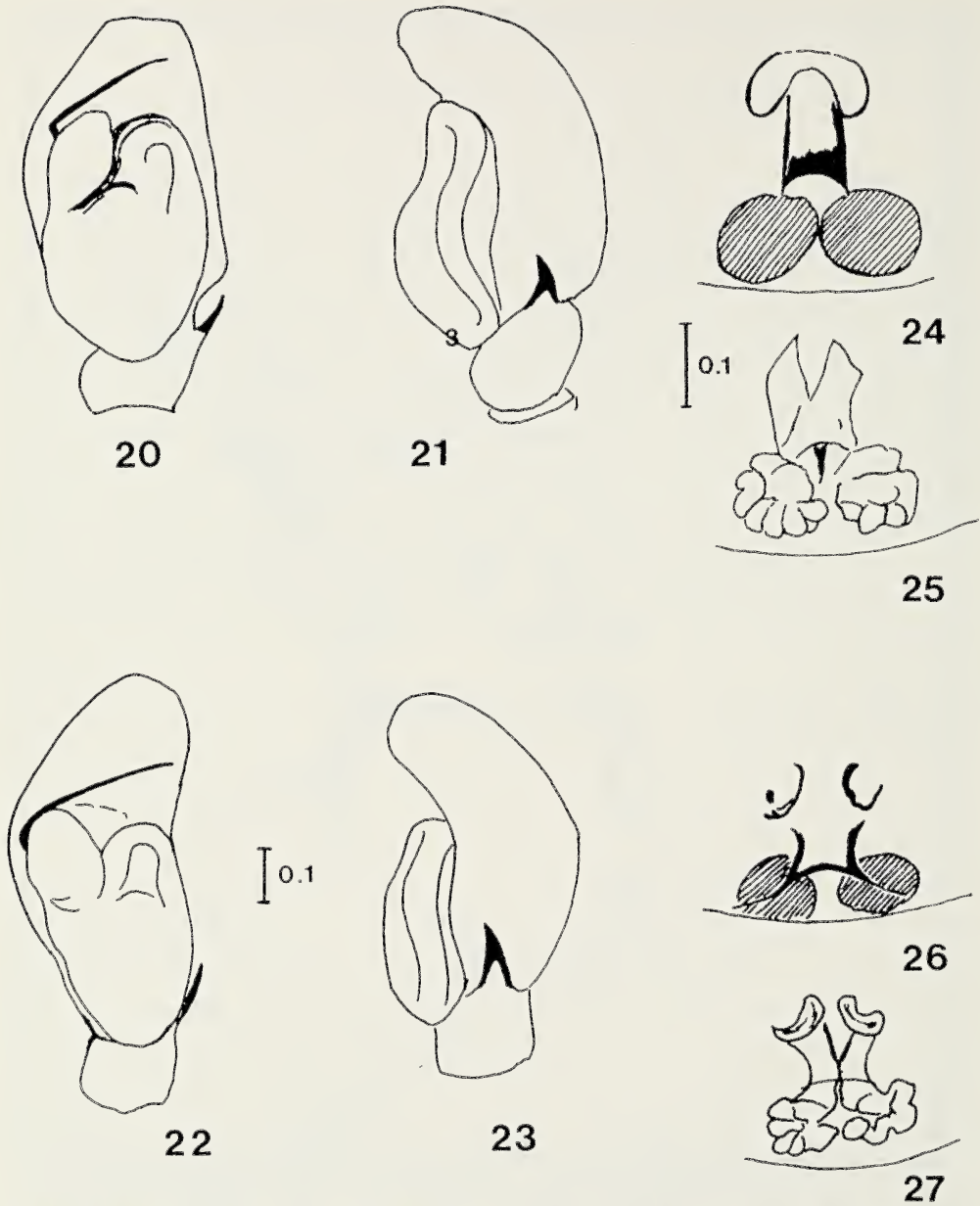
Variation.—Males differ in size and in length of the chelicerae (Fig. 28). There does not appear to be an allometric relationship between these two parameters and the plotted dots fit a straight line with the formula $y = 0.498697x + 1.194149$. Males of other species appear to have similar relationships between carapace and chelicera measurements (differing somewhat in placement along the curve and in the exact formula for the curve), and were represented by fewer data points. Because of these factors, the graph of *H. palmarum* measurements is presented here as a representative for the genus. Generally the pattern of the carapace is relatively uniform, but both males and females have some variation in abdominal patterns; the males sometimes having central spots, but may lack them and the females sometimes have a herring-bone pattern or brown spots like female *H. mitrata*. There seems to be no geographic association with these patterns.

Natural history.—Males and females have been collected throughout the year, especially in the southern part of their range. Immatures seem to be also present throughout the year. This species is primarily associated with shrubs and small trees and has been collected on black mangroves, red mangroves, white mangroves, willows, scrub oaks and various understory shrubs in Florida. Females from Florida (most from black mangroves near Cedar Key, Levy Co.) produced an average of 15.1 eggs in the laboratory (range 6 to 27, SD = 5.5, $n = 24$) from March through October. Populations on black mangrove were relatively dense throughout the year in 1975. This species is often found sympatrically with *H. grenada* (Peckham and Peckham), but the latter is almost always found on saw palmettoes or dwarf *Sabal* palms. *Hentzia mitrata* (Hentz) is also found sympatrically with *H. palmarum* and long series of both species were collected in Bucks Co., Pennsylvania by Wilton Ivie, unfortunately without any ecological notes. Males of *H. palmarum* exhibit a characteristic courtship and agonistic display (described by Richman 1982).



Map 1.—North and Central America, showing distribution of *Hentzia palmarum* (closed circles, open circles = state record only), *H. poenitens* (closed square), *H. pima* (open square), and *H. fimbriata* (closed triangles).

Specimens examined.—(Material from Bruce Cutler Collection not examined marked with an asterisk) **BAHAMAS:** Great Exuma (UCB), Harbor Island (MCZ). **BERMUDA:** Grasmere (MCZ). **CANADA:** NOVA SCOTIA; Digby (CNC), Kentville (CNC). **ONTARIO:** London (CNC). **CUBA:** Cabanas (AMNH), Cristo (AMNH), Habana (AMNH, MCZ), Holguin (MCZ), Pinar Rio (AMNH), Santa Clara (AMNH), Santiago de Cuba (MCZ), San Vicente (AMNH), Soledad (MCZ). **MEXICO:** TAMAULIPAS; Reynosa (AMNH), Tampico (AMNH). **U.S.A.** (county records only, except for the District of Columbia): **ALABAMA:** Baldwin (AMNH), Mobile (AMNH). **ARKANSAS:** Bradley (EPC), Conway (EPC), Crawford (EPC), Hempstead (ANSP, AMNH, EPC), Jefferson (EPC), Mississippi (EPC), Perry (EPC), Washington (EPC, MCZ). **CONNECTICUT:** Fairfield (AMNH), Hartford (AMNH, USNMNH), Litchfield (AMNH, USNMNH), New Haven (AMNH, USNMNH),



Figures 20-27.—*Hentzia palmarum* (Hentz): 20, 21, palp of male from Levy Co., Fla., 20, ventral view; 21, retrolateral view; 22, 23, palp of male from Tulsa Co., Okla.; 22, ventral view; 23, retrolateral view; 24, 25, epigynum of female from Levy Co., Fla., 24, ventral view; 25, dorsal view; 26, 27, epigynum of female from Highlands Co., Fla., 26, ventral view; 27, dorsal view.

New London (AMNH). DELAWARE; *Sussex* (FSCA). DISTRICT OF COLUMBIA; "East Branch" (USNMNH). FLORIDA; *Alachua* (AMNH, FSCA), *Baker* (FSCA), *Bay* (FSCA), *Broward* (FSCA), *Citrus* (AMNH, FSCA), *Collier* (FSCA), *Dade* (AMNH, FSCA, MCZ), *Dixie* (FSCA), *Duval* (FSCA), *Escambia* (FSCA), *Gadsden* (FSCA, MCZ), *Glades* (AMNH), *Hendry* (FSCA), *Highlands* (AMNH, DBR, FSCA, MCZ, UCB), *Hillsborough* (FSCA), *Indian River* (FSCA), *Jackson* (AMNH, FSCA), *Jefferson* (MCZ), *Lake* (AMNH, FSCA), *Lee* (AMNH), *Leon* (AMNH, MCZ), *Levy* (EPC, FSCA), *Maddison* (MCZ), *Manatee* (FSCA), *Marion* (FSCA), *Martin* (AMNH, FSCA), *Monroe*

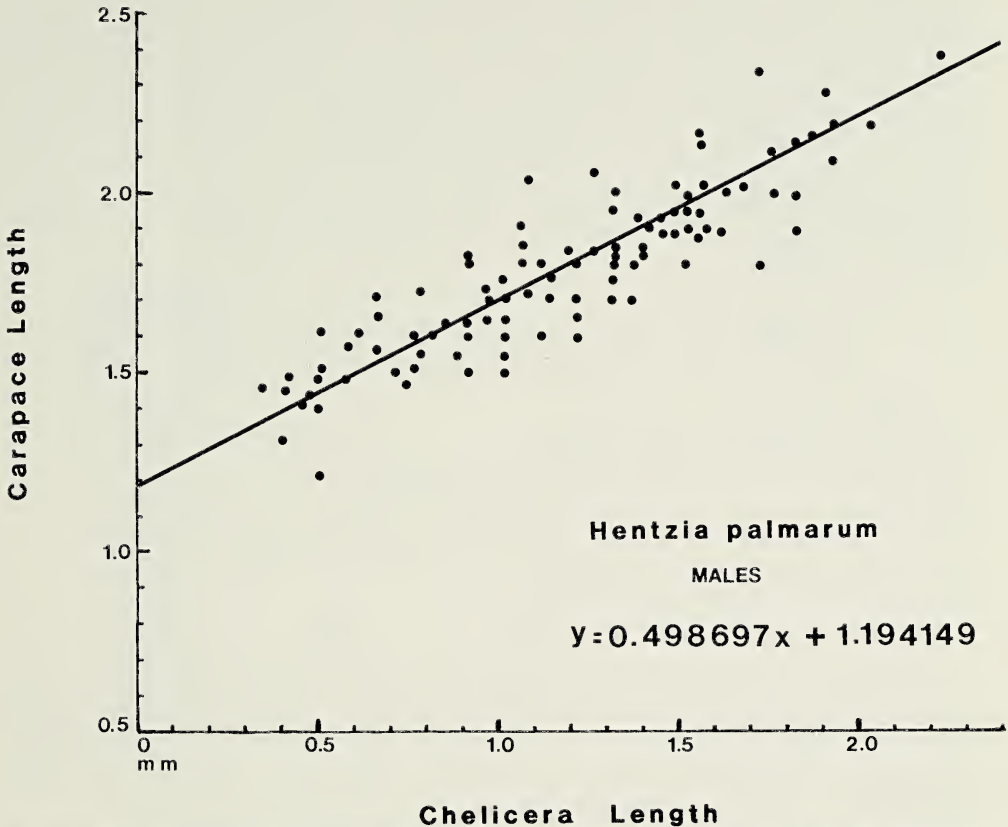


Figure 28.—Regression of carapace length vs. chelicera length for males of *Hentzia palmarum*, showing linear relationship and corresponding lack of allometry. Other species in the genus show similar regressions.

(AMNH, FSCA, MCZ, USNMNH), *Nassau* (AMNH), *Okaloosa* (AMNH, FSCA), *Orange* (AMNH, FSCA, USNMNH), *Palm Beach* (FSCA, MCZ), *Pasco* (FSCA), *Pinellas* (AMNH, EPC, FSCA, MCZ), *Polk* (FSCA), *Putnam* (FSCA), *St. Lucie* (FSCA), *Sarasota* (FSCA), *Seminole* (AMNH), *Volusia* (AMNH, FSCA), *Wakulla* (FSCA). GEORGIA; *Baker* (FSCA), *Bibb* (AMNH), *Brooks* (MCZ), *Charlton* (AMNH, FSCA), *Chatham* (AMNH), *Clarke* (MCZ), *Glynn* (AMNH, USNMNH), *Liberty* (AMNH), *Lowndes* (AMNH), *Morgan* (USNMNH), *Rayburn* (AMNH), *Screven* (AMNH), *Tift* (AMNH), *Turner* (AMNH), *Ware* (AMNH). ILLINOIS; *Fayette* (FSCA), *Jackson* (BC*) *Kane* (AMNH) *Hardin* (AMNH), *Madison* (FSCA). INDIANA; (state record only) (AMNH). IOWA; *Story* (AMNH), *Woodbury* (FSCA). KANSAS; *Bourbon* (AMNH), *Meade* (AMNH), *Sedgewick* (EPC). KENTUCKY; *Trigg* (FSCA) and state record (AMNH). LOUISIANA; *East Baton Rouge* (AMNH), *Iberville* (AMNH). MARYLAND; *Montgomery* (AMNH). MASSACHUSETTS; *Barnstable* (AMNH), *Hampshire* (AMNH), *Plymouth* (USNMNH), *Suffolk* (EPC), *Worcester* (MCZ). MICHIGAN; *Clinton* (FSCA), *Lenawee* (AMNH), *Livingston* (FSCA), *Macomb* (AMNH), *Midland* (AMNH), *Oakland* (AMNH), *St. Clair* (AMNH), *St. Joseph* (USNMNH), *Shiawassee* (BC*). MINNESOTA; *LeSeur* (BC*), *Wabasha* (BC*). MISSISSIPPI; *Forest* (AMNH), *George* (AMNH), *Hancock* (AMNH), *Harrison* (AMNH). MISSOURI; *Johnson* (EPC), *Newton* (EPC), *Phelps* (EPC), *Vernon* (EPC). NEBRASKA; *Dawson* (AMNH), *Jefferson* (DBR), *Hamilton* (DBR), *Harlan* (DBR). NEW JERSEY; *Bergen* (AMNH), *Burlington* (AMNH, MCZ), *Middlesex* (AMNH, CNC), *Ocean* (AMNH). NEW YORK; *Suffolk* (AMNH). NORTH CAROLINA; *Avery* (MCZ), *Dare* (CNC), *Durham* (AMNH), *Macon* (USNMNH), *New Hanover* (MCZ), *Wake* (AMNH). OKLAHOMA; *Carter* (AMNH), *Choctaw* (AMNH), *Comanche* (AMNH), *Grady* (AMNH), *Le Flore* (AMNH), *Marshall* (AMNH), *Payne* (DBR), *Pittsburgh* (AMNH), *Tulsa* (DBR). PENNSYLVANIA; *Bucks* (AMNH), *Carbon* (ANSP), *Centre* (MCZ) *Luzern* (ANSP), *Schuylkill* (USNMNH). SOUTH

CAROLINA; *Aiken* (AMNH), *Anderson* (CNC), *Berkeley* (USNMNH), *Charleston* (AMNH), *Dorchester* (AMNH), *Kershaw* (AMNH). TEXAS; *Aransas* (AMNH), *Austin* (AMNH), *Bell* (AMNH), *Bexar* (AMNH, MCZ), *Brazos* (TAM), *Cameron* (AMNH, MCZ), *Comal* (AMNH), *Dallas* (AMNH, USNMNH), *Erath* (TAM), *Grayson* (AMNH), *Gillespie* (AMNH), *Hidalgo* (AMNH, TAM, USNMNH), *Karnes* (MCZ), *Kenedy* (TAM), *Kerr* (AMNH, FSCA), *Limestone* (AMNH), *Llano* (AMNH), *Lubbock* (AMNH), *Medina* (AMNH), *McLennan* (AMNH), *San Patricio* (AMNH, FSCA, MCZ), *San Saba* (AMNH), *Shelby* (AMNH), *Travis* (ANSP, AMNH), *Walker* (TAM), *Wichita* (FSCA), *Wilbarger* (AMNH), *Williamson* (AMNH), *Uvalde* (AMNH). VIRGINIA; *Accomack* (USNMNH), *Arlington* (AMNH, USNMNH), *Augusta* (USNMNH), *Montgomery* (FSCA), *Norfolk* (MCZ).

Hentzia mitrata (Hentz)

Figs. 29-36, Map 2

Attus mitratus Hentz 1846:363 (type destroyed).

Attus morigerus Hentz 1846:365 (type destroyed).

Maevia sulphurea C. L. Koch 1848:71 (type not examined).

Maevia pallida C. L. Koch 1848:79 (type not examined).

Icius mitratus Peckham and Peckham 1888:48; Emerton 1891:232; 1902:57.

Anoka mitrata Peckham and Peckham 1894:125.

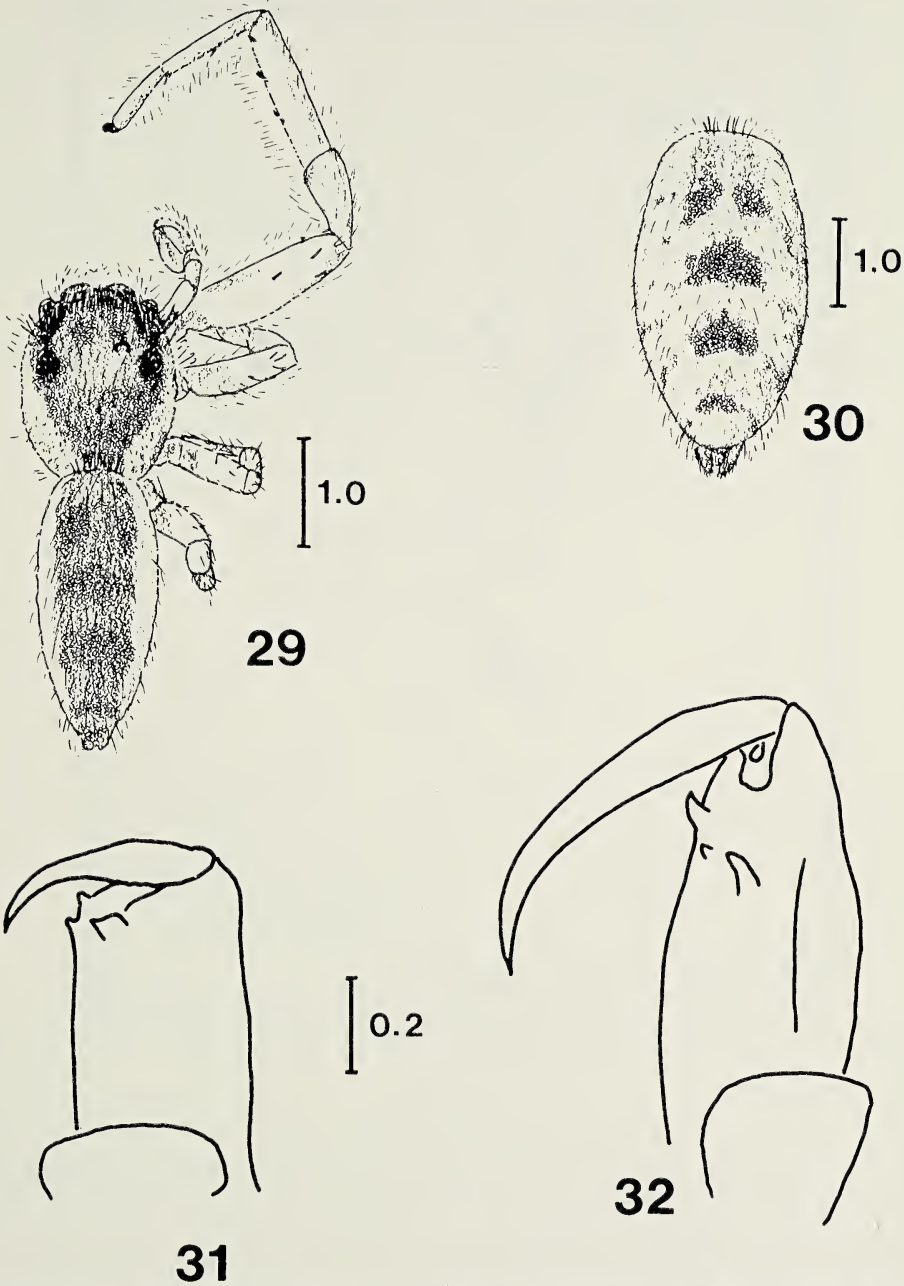
Wala mitrata Peckham and Peckham 1909:507.

H. mitrata Chickering 1944:159; Kaston 1948:492.

Diagnosis.—Male chelicerae generally short and lacking pigmentation, male first legs with white hair fringe and unpigmented (Fig. 29). Male palpus with bulb expanded toward distal end (Fig. 33). Female with elongate central bell-shaped structure on epigynum (Fig. 35), generally with legs unpigmented. These characteristics separate this species from all other members of the genus.

Male.—Total length 3.50-4.10. Carapace 1.50-1.70 long, 1.20-1.40 wide, 0.65-0.85 high at PLE. Ocular area 0.65-0.75 long, 0.90-1.02 wide anteriorly and 1.00-1.10 wide posteriorly. Chelicerae 0.50-0.60 long, 0.30-0.35 wide (10 males from NE of Jamison, Horseshoe Bend, Neshaminy Creek, Bucks Co., Pennsylvania). Carapace length and cheliceral length measurements (49 specimens from Quebec, Ontario, Georgia, New Jersey, Missouri, Mississippi, Florida and North Carolina) 1.45-2.05 and 0.50-1.15. The males with the longest chelicerae from Florida. PME equidistant between ALE and PLE. Leg formula 1423. Carapace orange with red-brown bands on either side of center, extending around eyes. Eyes ringed in black except AME which are ringed with brown. Clypeus covered with white hairs. Chelicerae whitish. Endites, labium and sternum yellow-cream. Abdomen yellow colored with brown markings (Fig. 29). Venter gray to cream. All legs yellow. Palpi yellow. In life males of this species from Florida appear to be white with white legs and orange dorsum.

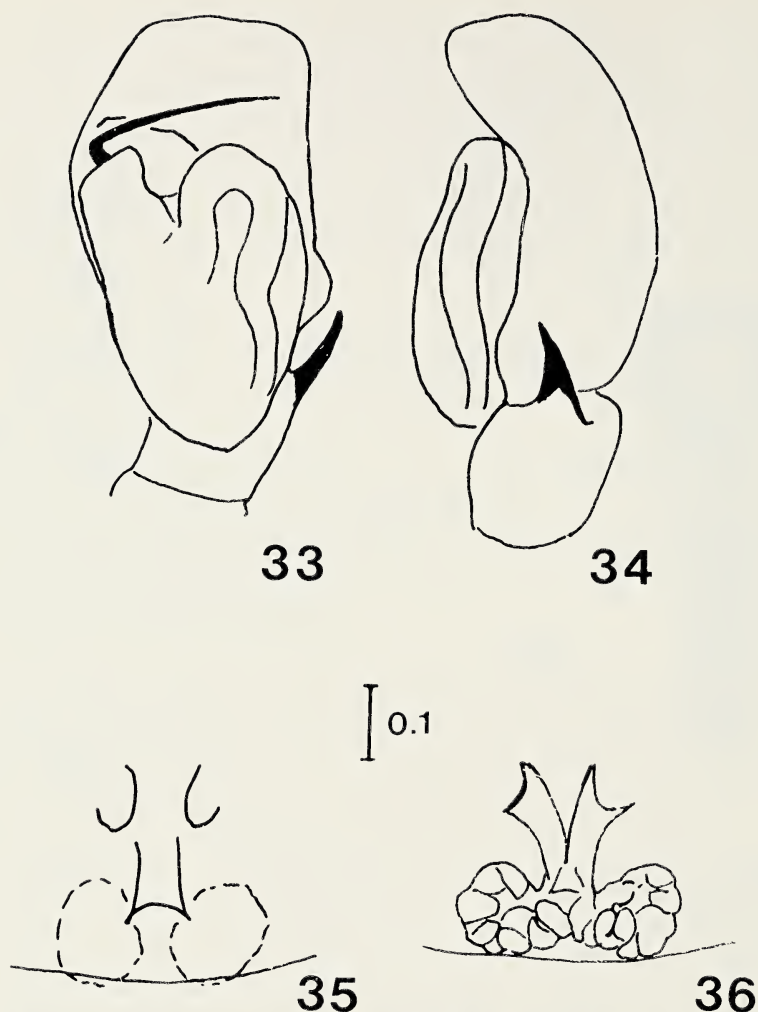
Female.—Total length 2.90-4.50. Carapace 1.50-1.80 long, 1.20-1.40 wide, 0.60-0.75 high at PLE. Ocular area 0.65-0.80 long, 0.95-1.12 wide anteriorly, 1.00-1.20 posteriorly. Chelicerae 0.40-0.50 long, 0.26-0.35 wide (10 females from NE of Jamison, Horseshoe Bend, Neshaminy Creek, Bucks Co., Pennsylvania). PME closer to ALE than to PLE. Leg formula 1423. Carapace orange-brown, covered with white hairs, scales. Clypeus covered with white hairs. Endites and labium lighter distally. Abdomen yellowish with brown pattern (Fig. 30). First legs orange. Other legs and palpi yellowish. In life females from Florida are white with brown markings on the body and white legs.



Figures 29-32.—*Hentzia mitrata* (Hentz): 29, male from Washington Co., Minn., dorsal view; 30, female from Washington Co., Minn., dorsal view of abdomen; 31, 32, ventral views of male left chelicera; 31, from Bucks Co., Penn., 32, from Dade Co., Fla.

Distribution.—Ontario and Quebec south to Florida and the Bahamas and west to eastern Texas and Minnesota (Map 2).

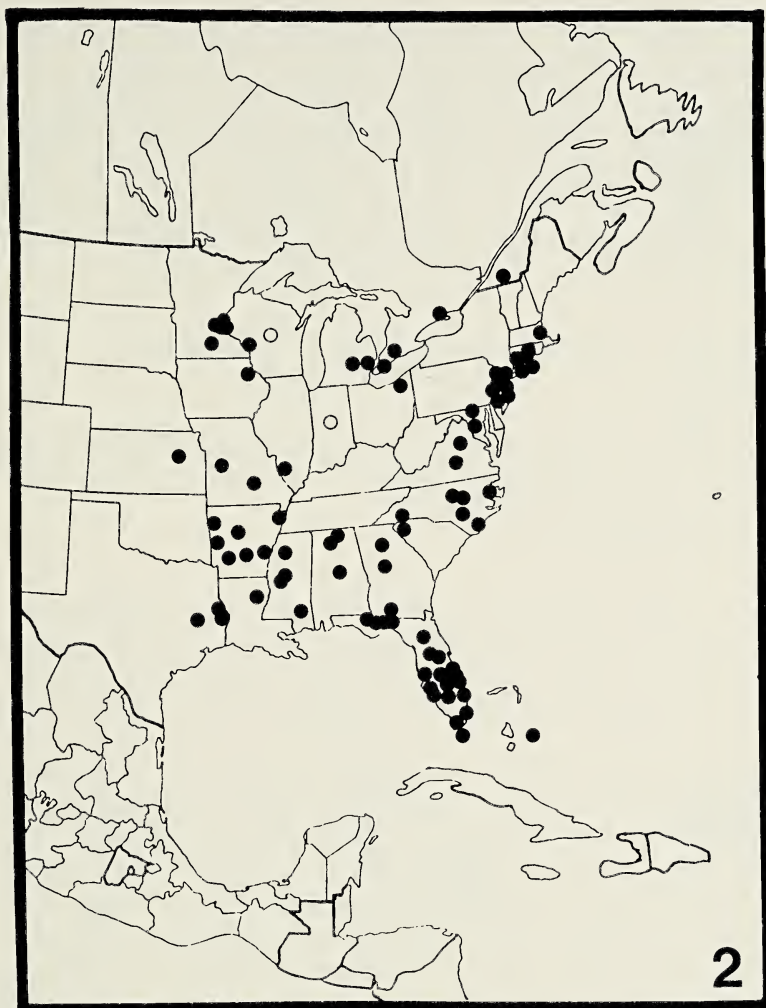
Variation.—Males generally have short chelicerae in most of the species range except in parts of Florida, where they may have chelicerae half as long as the carapace. Males from Florida tend to have sparser fringes on the first legs and



Figures 33-36.—*Hentzia mitrata* (Hentz): 33, 34, palp of male from Dade Co., Fla.; 33, ventral view; 34, retrolateral view; 35, 36, epigynum of female from Bucks Co., Penn.; 35, ventral view; 36, dorsal view.

narrower palpi, but otherwise match with more northern specimens. Females vary in the dorsal markings, with some similar to *H. palmarum* females. The epigyna are relatively uniform. Some specimens from Cuba (MCZ) may have to be assigned to this species, but I have not seen a male that looked exactly like mainland specimens. Until more material is available from Cuba, I feel that it is best to not include the records of *H. mitrata* from this island.

Natural history.—Adults have been collected in every month of the year, especially in the southern part of the range. They usually have been collected on shrubs, such as wax myrtle, or trees, such as live oak. Natural enemies include the wasp *Trypoxylon (Trypargilum) clavatum* Say (Hymenoptera: Sphecidae). Adults and immatures were found as prey in the nests of this wasp under a wooden bridge in Leon Co., Florida in July along with some *H. palmarum* (Coll. G. B. Edwards). The courtship behavior was described by Peckham and Peckham (1889, 1890) and Richman (1982).



Map 2.—North and Central America, showing distribution of *Hentzia mitrata*.

Specimens examined.—(Material from Bruce Cutler Collection not examined marked with an asterisk) **BAHAMAS:** Great Exuma (MCZ), Rum Cay (MCZ). **CANADA:** ONTARIO; Belleville (FSCA), Essex Co. (CNC), London (CNC), Pelee Island (AMNH), Turkey Point (FSCA). QUEBEC; Frelighsburg (CNC). **U.S.A.:** (County records only, except for the District of Columbia) **ALABAMA;** Baldwin (AMNH), Coosa (AMNH), Madison (AMNH), Morgan (AMNH). **ARKANSAS;** Arkansas (EPC), Conway (EPC), Hempstead (ANSP, EPC), Jefferson (EPC), Mississippi (EPC), Polk (EPC), Washington (EPC, MCZ). **CONNECTICUT;** London (AMNH), Middlesex (AMNH), New Haven (AMNH, USNMNH). **DISTRICT OF COLUMBIA;** “Chain Bridge” (USNMNH), “Battery” (USNMNH). **FLORIDA;** Alachua (FSCA, UCB), Dade (AMNH, FSCA, MCZ), Gadsden (MCZ), Glades (AMNH), Hernando (FSCA), Highlands (AMNH), Hillsborough (FSCA), Indian River (MCZ), Jackson (FSCA), Jefferson (MCZ), Lake (AMNH), Levy (FSCA), Leon (FSCA, MCZ), Martin (AMNH), Monroe (AMNH, FSCA), Orange (AMNH), Palm Beach (FSCA, MCZ), Pasco (FSCA), Polk (FSCA), St. Lucie (FSCA), Sarasota (FSCA). **GEORGIA;** Charleton (USNMNH), Dekalb (AMNH), Hall (AMNH, USNMNH), Thomas (CNC, DBR). **ILLINOIS;** St. Clair? (AMNH) also state record (AMNH). **INDIANA;** State record (AMNH). **IOWA;** Clayton (MCZ). **KANSAS;** Riley (FSCA). **LOUISIANA;** Madison (AMNH). **MARYLAND;** Montgomery (AMNH, USNMNH). **MASSACHUSETTS;** Plymouth (USNMNH), Suffolk (MCZ). **MICHIGAN;** Livingston (FSCA), St. Claire (AMNH), Shiawassee (BC*). **MINNESOTA;** Anoka (FSCA), Blue Earth (MCZ), Chisago (BC*), Hennepin (BC*), Ramsey (BC*), Wright (BC*), Washington (DBR). **MISSISSIPPI;** Forest

(AMNH), *Humphreys* (AMNH), *Panola* (EPC), *Sharkey* (EPC). MISSOURI; *Johnson* (EPC), *Phelps* (EPC). NEW JERSEY; *Bergen* (AMNH), *Burlington* (AMNH), *Camden* (CNC), *Hunterdon* (AMNH), *Middlesex* (CNC, FSCA), *Monmouth* (AMNH), *Ocean* (AMNH), *Sussex* (AMNH), *Warren* (FSCA). NEW YORK; *Suffolk* (AMNH). NORTH CAROLINA; *Cumberland* (FSCA), *New Hanover* (MCZ), *Orange* (AMNH), *Transylvania* (MCZ), *Wake* (AMNH), *Washington* (MCZ). OHIO; *Lake* (AMNH). PENNSYLVANIA; *Bucks* (AMNH), *Philadelphia* (ANSP). SOUTH CAROLINA; *Oconee* (AMNH). TEXAS; *Jasper* (AMNH), *Sabine* (MCZ), *Walker* (TAM). VIRGINIA; *Amherst* (CNC, FSCA), *Arlington* (USNMNH), *Campbell* (USNMNH), *Fairfax* (USNMNH), *Montgomery* (USNMNH), *Page* (AMNH). WEST VIRGINIA; *Hamshire* (AMNH). WISCONSIN; *LaCrosse* (FSCA), *St. Croix* (BC*), and state record (MCZ).

Hentzia fimbriata (F. O. P. - Cambridge)

Figs. 37-43, Map 1

Anoka fimbriata F. O. P. - Cambridge 1901:256 (types from Guatemala in BMNH examined).

Anoka grenada F. O. P. - Cambridge 1901:256 (not *Anoka grenada* Peckham and Peckham 1894) (specimens from Guatemala in BMNH examined).

Wala fimbriata Petrunkevitch 1911:716.

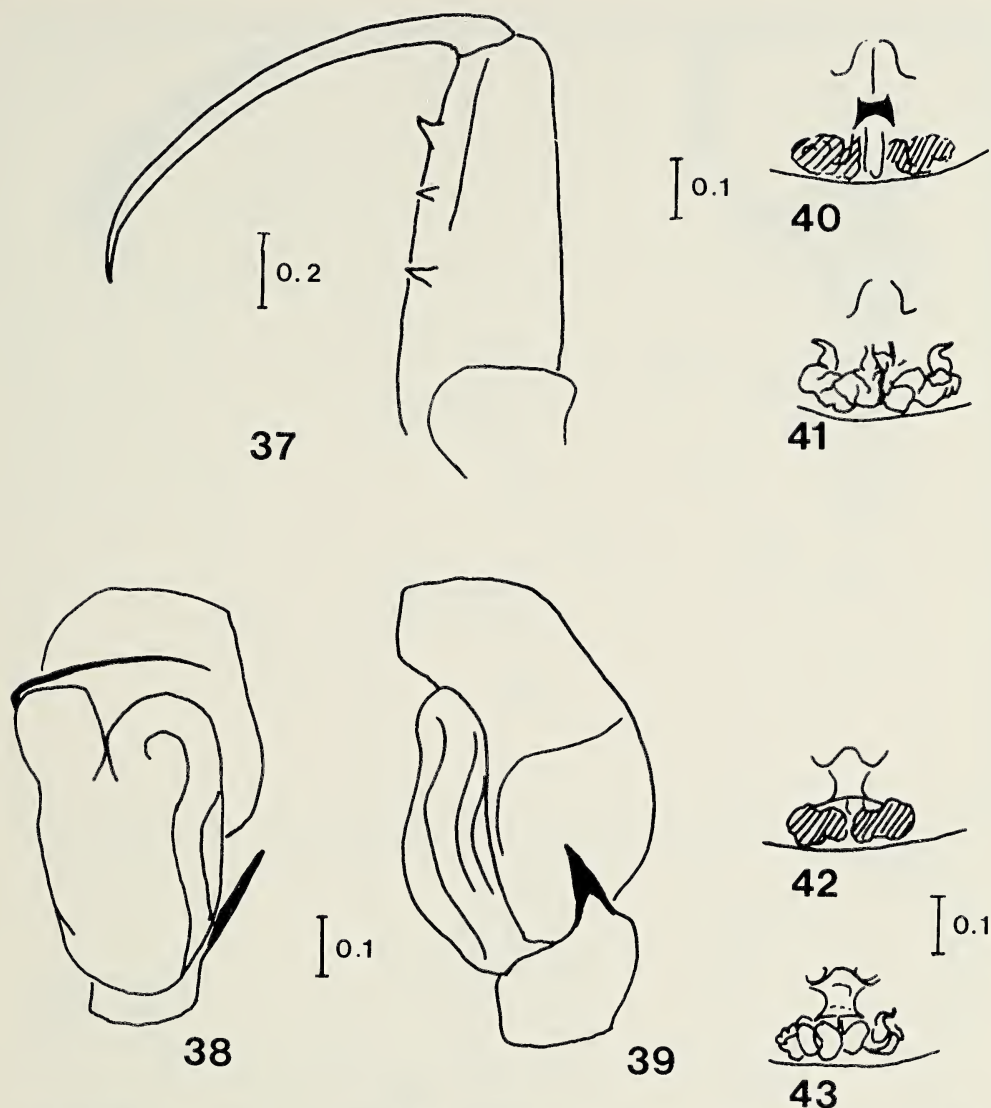
H. fimbriata Roewer 1954:1217.

Diagnosis.—Male similar to *H. palmarum* but with retromarginal cheliceral tooth separated from the first promarginal by at least the distance between promarginal teeth as seen ventrally (Fig. 37). Female with characteristic bell-shaped central epigynal structure with a “hump” between lateral openings (Figs. 40-43).

Male.—Total length 3.10-4.90. Carapace 1.50-1.90 long, 1.15-1.60 wide, 0.60-0.80 high at PLE. Ocular area 0.60-0.80 long, 0.95-1.20 wide anteriorly and 1.00-1.30 wide posteriorly. Chelicerae 0.50-1.50 long, 0.30-0.50 wide (14 males from Guatemala, Mexico and Nicaragua). Carapace and cheliceral length measurements (23 males from Mexico and Central America) 1.50-2.38 and 0.50-1.89. Males of Cambridge’s “*grenada*” with long chelicerae as opposed to his type specimens of *A. fimbriata*. As far as is known there are no valid records for *H. grenada* from Central or South America (see description of *H. grenada*). PME slightly closer to ALE than to PLE. Leg formula 1423. Carapace yellow, with lateral bands of white hairs. Black around all eyes but AME; brown around AME. Clypeus with white hairs. Chelicerae red to yellow-brown. Endites and labium yellow brown. Sternum orange-brown. Abdomen yellow with or without darker markings. First legs yellow-brown, darker on anterior ventral femora, patellae and tibiae. Other legs yellow. Pedipalpi yellow with dark spot on distal patellae.

Female.—Total length 3.60-5.15. Carapace 1.40-2.15 long, 1.10-1.40 wide, 0.50-0.70 high at PLE. Ocular area 0.60-0.75 long, 0.88-1.50 wide anteriorly and 0.95-1.15 wide posteriorly. Chelicerae 0.30-0.40 long, 0.20-0.30 wide (14 females from Guatemala, Mexico and Nicaragua). PME closer to ALE than to PLE. Leg formula 1423. Carapace orange with white hairs laterally. Black around eyes except AME. Brown around AME. Clypeus covered with white hairs. Chelicerae orange. Endites and labium orange. Sternum orange. Abdomen light brown with gray-brown markings. Venter yellow. First legs yellow to orange. Pedipalpi yellow.

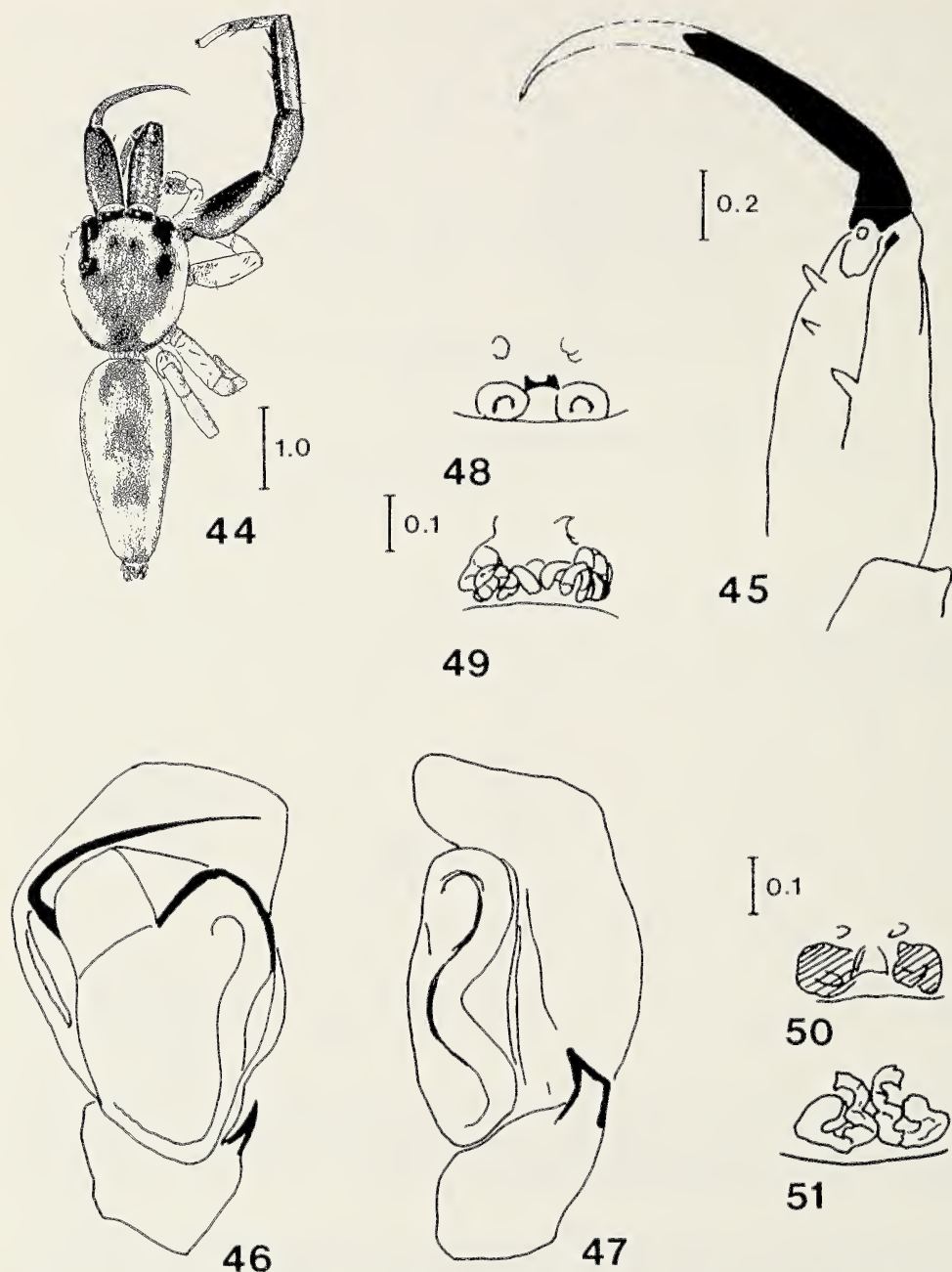
Distribution.—East coast of Mexico from southern Tamaulipas south to Colombia and north along the West coast to Nayarit (Map 1).



Figures 37-43.—*Hentzia fimbriata* (F. O. P.-Cambridge): 37-39, "Syntype" male from Guatemala; 37, left chelicera, ventral view; 38, palp, ventral view; 39, palp, retrolateral view; 40, 41, epigynum of female from Panzos, Guatemala; 40, ventral view; 41, dorsal view; 42, 43 epigynum of female from Campeche, Mexico; 42, ventral view; 43, dorsal view.

Natural history.—Males have been collected in January, March and June-November. Females have been collected in February-March, May-August and October. Adults probably can be found through the year, as with *H. palmarum*. Specimens from Veracruz were collected by W. Maddison on bushes along roadside in marsh.

Specimens examined.—**COLOMBIA:** Isla San Andres (UCR). **COSTA RICA:** GUANACASTE; 4 km NW Canyas (UCB), Comunidad (MCZ). **GUATEMALA:** Amatitlan (AMNH), Panzos (AMNH), Petapa (BMNH), Rabinal (AMNH). **HONDURAS:** Roatan (FSCA). **MEXICO:** CAMPECHE; 6 km W Francisco Escarcega (MCZ). COLIMA; Santiago (AMNH). NAYARIT; Tepic (AMNH). OAXACA; Soledad (AMNH), 13 km S Tuxtepec (MCZ). SAN LUIS POTOSI; 20 mi. E Ciudad del Maiz (AMNH), Tamazunchale (AMNH). TAMAULIPAS; Nacimiento del Rio Frio nr. Gomez Farias



Figures 44-51.—*Hentzia tibialis* Bryant: 44, male from San Vicente, Cuba, dorsal view; 45, left chelicera of male from Pinar, Cuba, ventral view; 46, 47, palp of male from Soledad, Cuba; 46, ventral view; 47, retrolateral view; 48, 49 epigynum of female from San Vicente, Cuba; 48, ventral view; 49, dorsal view; 50, 51, epigynum of female from Habana, Cuba; 50, ventral view; 51, dorsal view.

(MCZ), 34 km E Tula (MCZ). VERACRUZ; Alamo (AMNH), 40 km E Coatzacoalcos (MCZ), Rio Blanco (MCZ), San Rafael (MCZ), Tlacotalpan (AMNH). YUCATAN; Grutas de Lolton 7 km S Oxkutzca (MCZ), 12 km N Pisté (MCZ), Uxmal (AMNH). NICARAGUA: Granada (MCZ), Masachapa (AMNH).



Map 3.—West Indies, showing distribution of *Hentzia antillana* (closed circles) and *H. tibialis* (open circles).

Hentzia tibialis Bryant

Figs. 44-51, Map 3

Balmaceda peckhami Bryant 1940:464 (holotype female from Soledad, Cuba, in MCZ examined - *Hentzia peckhami* preoccupied by *Anoka p.* Cockerell 1893). NEW SYNONYMY.

H. tibialis Bryant 1940:498 (holotype male from Soledad, Cuba, in MCZ examined, allotype female = *H. chekika* n. sp.).

Diagnosis.—Males differ from all other *Hentzia* spp. in having a truncated tibial apophysis on the palpus (Fig. 47). Otherwise they resemble *H. palmarum* in general structure. The apparent female is *Balmaceda peckhami* Bryant. The female paired by Bryant (1940) with *H. tibialis* is *H. chekika* n. sp. The female of *H. tibialis* differs from all other *Hentzia* in having wide spaced openings in the epigynal plate and in the structure of the spermathecal ducts (Figs. 48-51).

Male.—Total length 3.90-4.92. Carapace 1.35-1.89 long, 1.35-1.80 wide, 0.70-0.86 high at PLE. Ocular area 0.70-0.82 long, 1.05-1.23 wide anteriorly and 1.10-1.31 wide posteriorly. Chelicerae 0.90-1.89 long, 0.35-0.53 wide (five males from Cuba). PME closer to ALE than to PLE. Leg formula 1432 (leg 3 and 2 very close in length). Carapace red-brown with white hairs laterally. Black around eyes except dark brown around AME. Clypeus red-brown. Chelicerae red-brown with anterolateral dark brown line. Fang black with distal 1/4 yellow. Endites and labium dark brown. Sternum orange. Abdomen orange-brown covered with

iridescent scales, white laterally. Venter brown; epigastric furrow with lateral orange streaks. First legs red-brown, darker anteroventrally. Tarsi yellow. Other legs orange. Pedipalpi yellow; bulb very dark, almost black.

Female.—Total length 3.40-4.65. Carapace 1.40-1.70 long, 1.10-1.38 wide, 0.60-0.80 high at PLE. Ocular area 0.65-0.85 long, 0.95-1.18 wide anteriorly and 1.00-1.25 wide posteriorly. Chelicerae 0.40-0.50 long, 0.25-0.35 wide (seven females from Cuba). PME closer to ALE than to PLE. Leg formula 1423 (leg 1 and leg 4 close in length). Carapace orange-brown with white scales and hairs laterally. Black around eyes except brown around AME. Clypeus covered with white hairs. Chelicerae orange to red-brown. Endites and labium orange-brown with lighter tips. Sternum orange to brown. Abdomen yellow with darker brown central band of block-like markings. Lateral areas with brown blotches. Venter yellow. First legs yellow-brown, darker around distal patellae, tibiae and metatarsi; tarsi yellow. Other legs yellow. Pedipalpi yellow with proximal half annulae except on femora.

Distribution.—Known only from Cuba (Map 3).

Natural history.—Males collected from May and July-September. Females collected from February and July.

Specimens examined.—CUBA: Habana (MCZ), Luis Lazo (MCZ), Pinar del Rio (AMNH), San Vicente (AMNH), Soledad (MCZ).

Hentzia audax Bryant

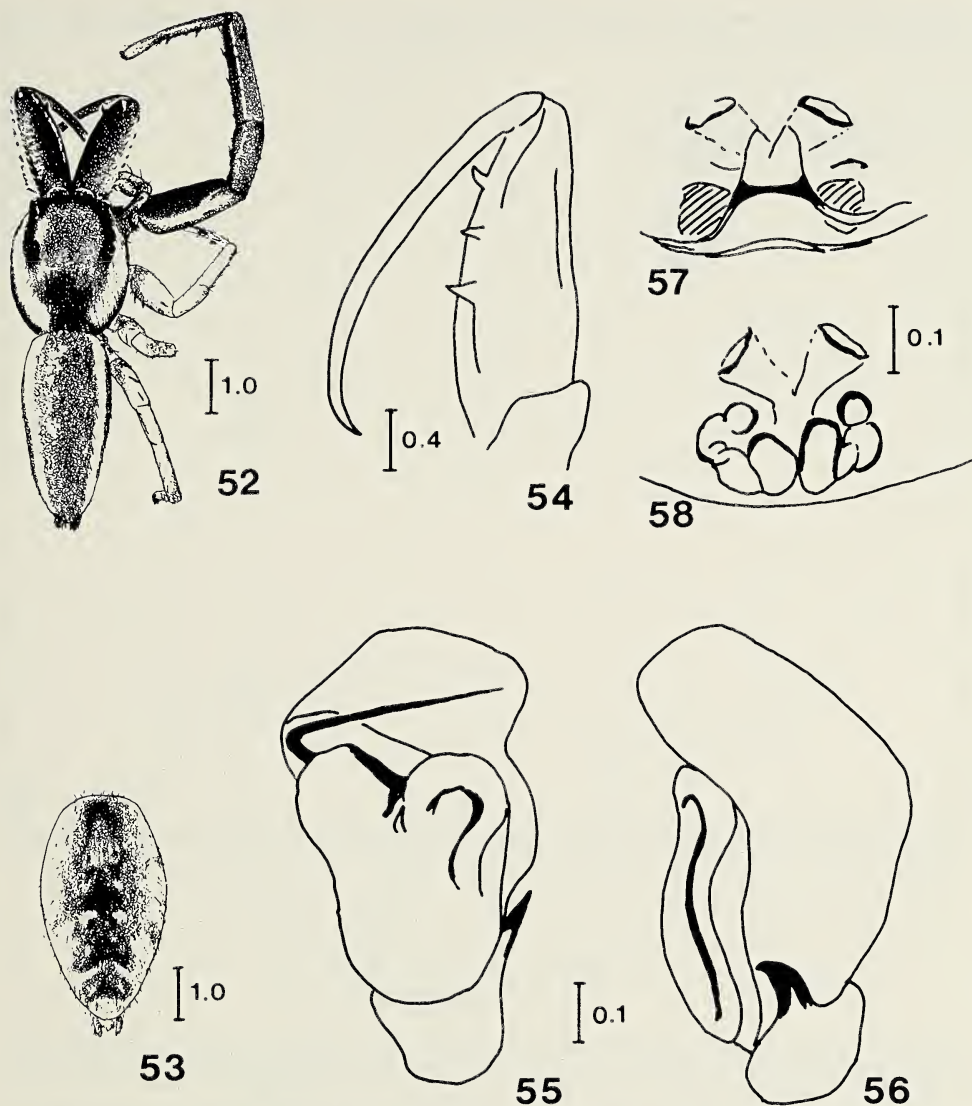
Figs. 52-58, Map 4

Hentzia audax Bryant 1940:496 (holotype male and allotype female from Pico Turquino, Cuba in MCZ examined).

Diagnosis.—Males differ from other members of the genus, except *H. cubana*, by the curved and often massive tibial apophysis on the palpus (Figs. 55, 56) and the pattern of cheliceral teeth (Fig. 54). It differs from *H. cubana* in being much larger (over 5.25 mm as opposed to 3-4 mm) and in the structure of the palp (Figs. 55, 56). The female epigynum differs from that of *H. cubana* in having trumpet-like straight lateral tubes, with slit-like openings (Figs. 57, 58).

Male.—Total length 5.30-6.00. Carapace 2.30-2.54 long, 1.90-2.10 wide, 0.90-1.10 high at PLE. Ocular area 0.90-1.10 long, 1.35-1.45 wide anteriorly, 1.45-1.60 wide posteriorly. Chelicerae 1.60-2.40 long, 0.60-0.66 wide (six males from Pico Turquino, Cuba). PME closer to ALE than to PLE. Leg formula 1423. Carapace red-brown, with yellow area between eyes and dark around eyes. White scales laterally. Clypeus and chelicerae red-brown. Endites and labium light red-brown. Sternum light red-brown to yellow-brown. Abdomen yellow-brown with an iridescent sheen caused by scales. Faint dorsal markings, lateral white lines. Venter yellow. First legs red-brown, slightly lighter on dorsal proximal femora and on tarsi. Other legs yellow. Pedipalpi red-brown, cymbium darker.

Female.—Total length 6.07-6.80. Carapace 2.20-2.21 long, 1.80-2.00 wide, 1.10-1.15 high at PLE. Ocular area 0.90-1.05 long, 1.39-1.45 wide anteriorly and 1.64-1.65 wide posteriorly. Chelicerae 0.82-0.90 long, 0.49-0.60 wide (two females Pico Turquino, Cuba). PME slightly closer to ALE than to PLE. Leg formula 1423.



Figures 52-58.—*Hentzia audax* Bryant, types from Pico Turquino, Cuba: 52, 53, paratypes; 52, male, dorsal view; 53, female, dorsal view of abdomen; 54, left chelicera of male holotype, ventral view; 55, 56, palp of male paratype; 55, ventral view; 56, retrolateral view; 57, 58, epigynum of female paratype; 57, ventral view; 58, dorsal view.

Carapace red-brown; yellow areas between eyes; eyes dark. Chelicerae red-brown. Endites and labium red-brown. Sternum yellow-brown. Abdomen yellow with central pattern of brownish anterior paired streaks, followed by three central streaks or triangles. Venter yellow. First legs red-brown. Other legs yellow. Pedipalpi red-brown with yellow tips.

Distribution.—Known only from mountains and coast of southeastern Cuba. (Map 4)

Natural history.—Males and females collected in June.

Specimens examined.—CUBA: Pico Turquino (MCZ), coast below Pico Turquino (MCZ).



Map 4.—West Indies and Florida, showing distribution of *Hentzia grenada* (closed circles), *H. mandibularis* (open circles), *H. audax* (closed squares), and *H. vernalis* (closed triangles).

***Hentzia cubana*, new species**

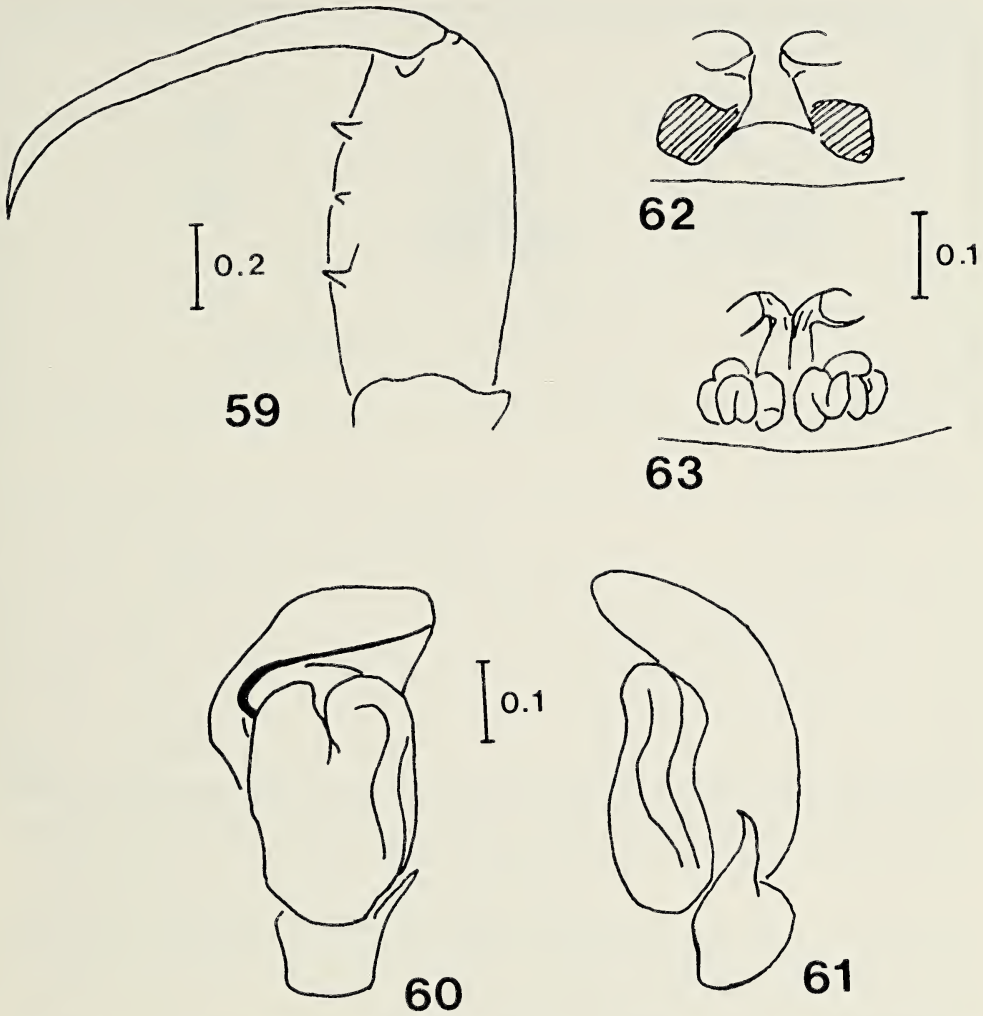
Figs. 59-63, Map 5

Types.—Holotype male and allotype female from Soledad, Cuba (August 1931, N. Banks) deposited in the Museum of Comparative Zoology.

Etymology.—The name is derived from the island on which the species occurs.

Diagnosis.—Males differ from all other species of *Hentzia* except *audax* in having a hooked tibial apophysis combined with nearly equidistant cheliceral teeth. They differ from *H. audax* in being much smaller (less than 4 mm), in the more slender tibial apophysis of the male pedipalp (Figs. 60, 61), and in the associated females. Females differ from all other species in the details of the epigynum (Figs. 62, 63). This species may prefer the lowlands more than *H. audax*.

Male.—Total length 3.25-3.75. Carapace 1.35-1.55 long, 1.10-1.30 wide, 0.60-0.75 high at PLE. Ocular area 0.60-0.75 long, 0.90-1.10 wide anteriorly and 1.00-1.12 wide posteriorly. Chelicerae 0.40-1.10 long, 0.30-0.42 wide (seven males from Soledad, Cuba). PME closer to ALE than to PLE. Leg formula 1423. Carapace red-brown with lateral white scales. Black around eyes except red-brown around AME. Clypeus covered with white hairs. Chelicerae red-brown. Endites very dark, with anterolateral edge white. Labium dark brown, tip white. Sternum



Figures 59-63.—*Hentzia cubana* n. sp. from Cuba: 59, left chelicera of male, ventral view; 60, 61, palp of male from Soledad, 60, ventral view; 61, retrolateral view; 62, 63, epigynum of female; 62, ventral view; 63, dorsal view.

orange. Abdomen brown, with shiny scales; laterally lighter. Venter light brown. First legs red-brown; tarsus and metatarsus lighter and metatarsus with slightly darker distal end. Other legs yellow-orange. Pedipalps orange-brown, cymbium lighter.

Female.—Total length 4.20-5.00. Carapace 1.55-1.90 long, 1.28-1.60 wide, 0.65-0.75 high. Ocular area 0.70-0.80 long, 1.08-1.20 wide anteriorly and 1.10-1.30 wide posteriorly. Chelicerae 0.40-0.55 long, 0.30-0.40 wide (five females from Soledad, Cuba). PME equidistant between ALE and PLE. Leg formula 1423. Carapace orange-brown; white scales laterally. Black around eyes except brown around AME. Clypeus covered with white hairs. Chelicerae orange. Endites and labium dark brown, with pale tips. Sternum dark brown. Abdomen yellowish with brown central band; central band with two light streaks forming inverted "V" anteriorly, followed by lateral notches near middle and narrowing into a triangular and then block-like mark toward posterior. Venter yellow. First legs



Map 5.—West Indies, showing distribution of *Hentzia whitcombi* (closed circles), *H. cubana* (open circles), *H. squamata* (closed square), and *H. calypso* (closed triangles).

orange-brown with tarsus-metatarsus lighter; metatarsus with darker distal ring. Other legs yellow-orange. Pedipalpi yellow with dark dorsal markings on proximal tarsus and tibia.

Distribution.—Known only from Cuba (Map 5).

Natural history.—Males collected in February-March, May, July-September and November. Females in February-March and July-August. As in other tropical species, adults are probably found throughout the year.

Specimens examined.—CUBA: Buenos Aires (MCZ), Cienaga de Zapata (MCZ), Habana (MCZ), Pinar del Rio (MCZ), Punta San Juan (MCZ), Soledad (MCZ), 5 mi. E of Soledad (MCZ), Trinidad Mountains (MCZ).

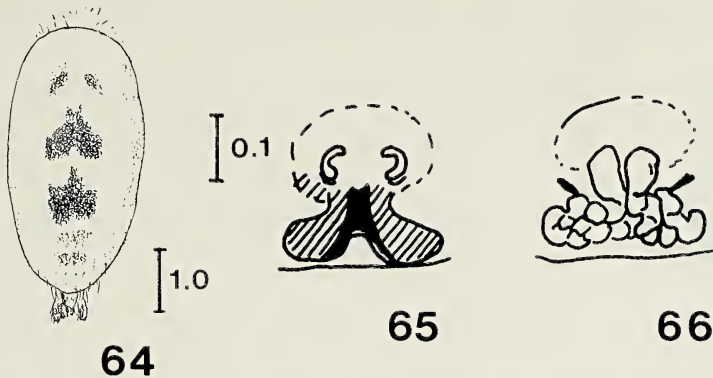
Hentzia pima, new species

Figs. 64-66, Map 1

Types.—Holotype female from Brown Canyon, Baboquivari Mountains, Pima Co., Arizona (8 June 1958, W. J. Gertsch) deposited in the American Museum of Natural History. The male is not known.

Etymology.—The name is derived from the American Indian tribe which also gave the name to the county.

Diagnosis.—Different from all other members of the genus in the c-shaped



Figures 64-66.—*Hentzia pima* n. sp., female holotype from Brown Canyon, Baboquivari Mts., Pima Co., Ariz.; 64, dorsal view of abdomen; 65, 66, epigynum; 65, ventral view; 66, dorsal view.

epigynal openings (Figs. 65, 66). Dorsal abdominal pattern (Fig. 64) similar to other members of the *palmarum* group.

Female.—Total length 5.61. Carapace 2.12 long, 1.77 wide, 0.89 high at PLE. Ocular area 0.89 long, 1.30 wide anteriorly and 1.48 wide posteriorly. Chelicerae 0.77 long, 0.47 wide (only holotype). PME closer to ALE than to PLE. Leg formula 1423. Carapace orange with scattered black hairs and white scales laterally. Dark around eyes. Clypeus covered with white hairs. Chelicerae orange, red-brown ventrally. Endites red-brown with white prolateral edges. Labium red-brown. Sternum orange. Abdomen yellow with distinctive brown markings consisting of two curved v-shaped marks in center of dorsum (Fig. 64). First legs orange. Other legs and pedipalpi yellow.

Distribution.—Known only from southern Arizona (Map 1).

Natural history.—Holotype collected in June.

Specimens examined.—Only from the type locality (AMNH).

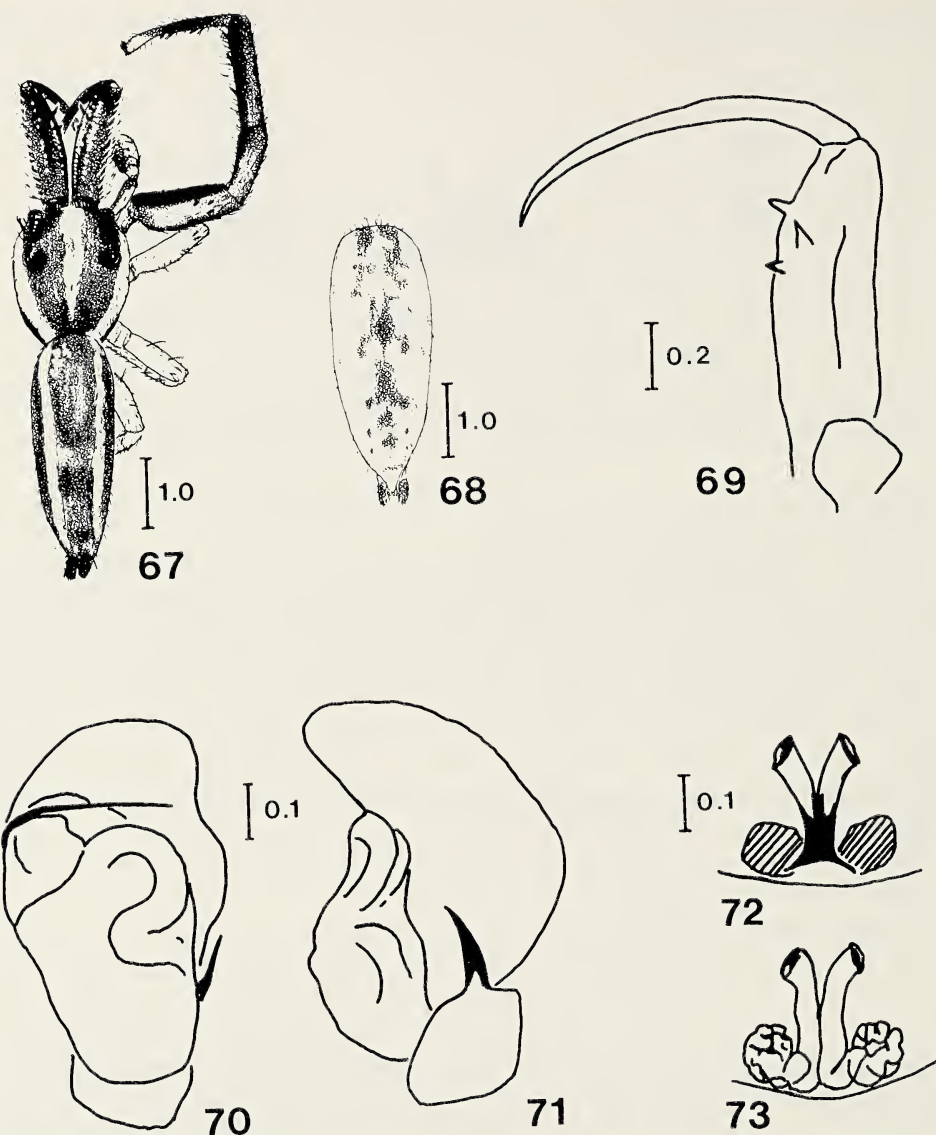
GRENADA SPECIES GROUP

The *grenada* species group consists of only three species, *H. grenada*, *H. chekika* and *H. poenitens*. They have distinctive female epigyna (Figs. 72, 73, 78, 79, 85, 86), with elongate to short J-shaped tubes leading to the spermathecae. Males of *H. grenada* differ from other members of the species group and from all other known *Hentzia* males by having a sperm tube loop in the bulb (Figs. 70, 71). It also differs from the other two species in the species group by the length of the female J-shaped tubes. The possible relationship of these three species is indicated on the cladogram (Fig. 15). Both *H. grenada* and *H. chekika* are very elongate, with moderately long chelicerae in large males. *Hentzia poenitens* is one of the smallest of the species of *Hentzia* and is widely separated geographically from the other species, being found in Sonora on the west coast of Mexico.

Hentzia grenada (Peckham and Peckham)

Figs. 67-73, Map 4

Anoka grenada Peckham and Peckham 1894:126 (holotype male from "New Grenada" in MCZ examined).



Figures 67-73. *Hentzia grenada* (Peckham and Peckham): 67, 68, 70-73, from Highlands Co., Fla.; 67, male, dorsal view; 68, female, dorsal view of abdomen; 69, left chelicera of holotype male from "New Grenada", ventral view; 70, 71, palp of male; 70, ventral view; 71, retrolateral view; 72, 73, epigynum of female; 72, ventral view; 73, dorsal view.

Wala grenada Banks 1904:138; Peckham and Peckham 1909:507.

H. grenada Roewer 1954:1217.

Diagnosis.—Males differ from all other members of the genus by the presence of a loop in the sperm duct as viewed from the retromargin of the palpal bulb (Figs. 70, 71). Females have a characteristic epigynal structure, including two long, slightly J-shaped ducts (Figs. 72, 73). Both males and females have very elongate bodies and males possess a white band on the central dorsal carapace which widens toward the eyes (Fig. 67). Only *H. chekika* has a similar appearance, but the latter species is larger, lives on tall palm trees and differs in

lacking the loop on the bulb of the male palpus and in the structure of the female epigynum.

Male.—Total length 4.08-5.70. Carapace 1.58-1.80 long, 1.20-1.70 wide, 0.66-0.80 high at PLE. Ocular area 0.65-0.90 long, 1.00-1.23 wide anteriorly and 1.00-1.23 wide posteriorly. Chelicerae 0.90-1.80 long, 0.30-0.48 wide (10 males from Highlands and Martin counties, Florida). PME slightly closer to ALE than to PLE. Leg formula 1423. Carapace red-brown with central band of white scales and hairs widening toward AME. Lateral white band followed by marginal dark band. Black around eyes except brown around AME. Clypeus covered with white hairs. Chelicerae dark red-brown, fangs lighter on distal 1/3. Endites and labium dark brown. Sternum orange. Abdomen yellow dorsally with red-brown markings (Fig. 67). Venter light brown with lateral areas lighter. First legs yellow with red-brown prolateral and retrolateral femora, distal patellae, distal and proximal tibiae. Other legs yellow. Pedipalpi red-brown with cymbium yellow.

Female.—Total length 4.10-5.50. Carapace 1.60-2.00 long, 1.20-1.52 wide, 0.55-0.80 high at PLE. Ocular area 0.70-0.90 long, 1.00-1.22 wide anteriorly and 1.05-1.28 wide posteriorly. Chelicerae 0.40-0.60 long, 0.28-0.42 wide (10 females from Highlands and Martin counties, Florida). PME slightly closer to ALE than to PLE. Leg formula 1423. Carapace orange, darker laterally back of eyes and lighter down middle and in band along either side. Margin line black. Black around eyes except brown around AME. Clypeus covered with white hairs. Chelicerae orange-brown. Endites and labium orange-brown with light distal tips. Sternum yellow. Abdomen yellow with brown markings (Fig. 68). Venter yellow. First legs yellow with brown retrolateral streak on femora and dark spots on the promargin of femora, distal and prolateral patellae, and distal and proximal tibiae. Other legs yellow. Pedipalpi yellow with dorsal spots on proximal patellae, tibiae and tarsi.

Distribution.—Florida and south Georgia (Map 4).

Discussion.—It appears that the type specimen of this species was mislabeled at some point, as it matches perfectly with males from Florida but does not compare with any specimens known from Central America, northern South America or the West Indies. New Grenada is now the modern state of Colombia. A similar problem was discovered with two of Keyserling's types (see *H. vittata*).

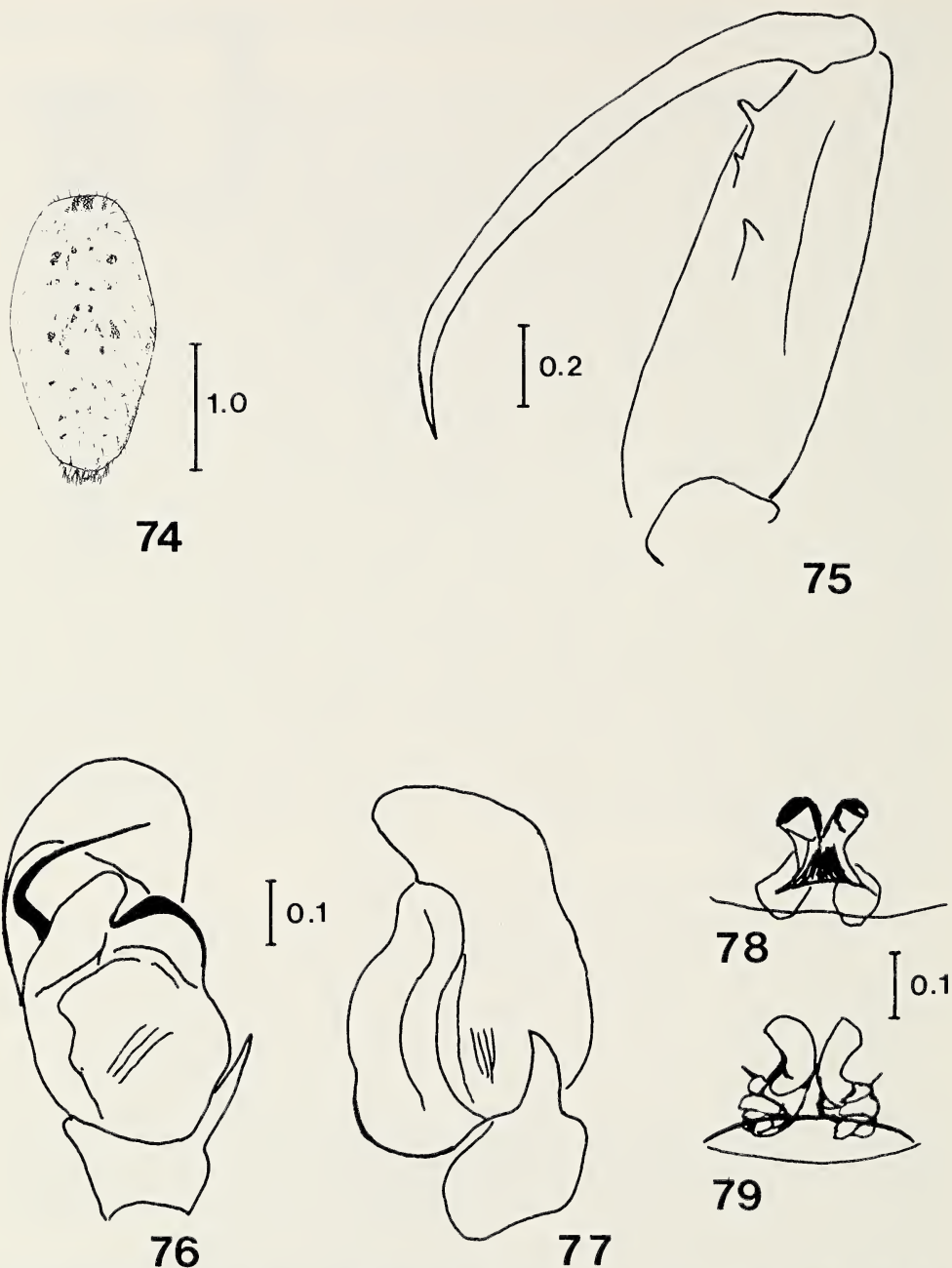
Natural history.—Males have been collected in every month but October and females from every month but January, August and October. There are thus probably adults throughout the year. The courtship is quite similar to that of *H. palmarum* and males will readily mate with females of the latter species under laboratory conditions (Richman 1982). Hybrids are unknown in the wild and immatures from crosses were not successfully raised in the laboratory.

Specimens examined.—U.S.A.: (County records only) FLORIDA; *Alachua* (FSCA), *Baker* (FSCA), *Collier* (AMNH, FSCA, MCZ), *Dade* (FSCA, MCZ), *Duval* (FSCA), *Gadsden* (FSCA), *Glades* (FSCA), *Hamilton* (AMNH), *Highlands* (AMNH, DBR, FSCA), *Hillsborough* (FSCA), *Indian River* (AMNH, FSCA), *Lake* (AMNH), *Lee* (AMNH), *Manatee* (DBR), *Marion* (FSCA), *Martin* (FSCA), *Monroe* (AMNH, FSCA, MCZ), *Pinellas* (FSCA), *Nassau* (FSCA), *Putnam* (FSCA). GEORGIA; *Chatham* (USNMNH), *Lowndes* (AMNH).

Hentzia poenitens (Chamberlin)

Figs. 74-79, Map 1

Wala poenitens Chamberlin 1924:680 (holotype male from Guaymas, Sonora, consisting of only the right palpus, in MCZ examined).



Figures 74-79.—*Hentzia poenitens* (Chamberlin) from Sonora, Mexico: 74, female from Los Algodones, dorsal view of abdomen; 75, left chelicera of male from Guaymas, ventral view; 76, 77, palp of male from Guaymas, 76, ventral view; 77, retrolateral view; 78, 79, epigynum of female from Los Algodones; 78, ventral view; 79, dorsal view.

H. poenitens Roewer 1954:1218.

Diagnosis.—Male palpus with slanted anterior bulb (Fig. 76) and internal structure of female epigynum with short J-shaped ducts diagnostic (Fig. 79). The smallest member of the genus other than *H. calypso*. Lacking markings.

Male.—Total length 3.60. Carapace 1.59 long, 1.30 wide, 0.65 high at PLE. Ocular area 0.71 long, 0.94 wide anteriorly and 1.06 wide posteriorly. Chelicerae 1.18 long, 0.41 wide (one male from Guaymas, Sonora). PME closer to ALE than to PLE. Leg formula 1423. Carapace orange with scattered black hairs; white scales laterally. Eyes as in other species of the group. Clypeus covered with white hairs. Chelicerae brown, darker and mottled ventrally; with corrugated iridescence. Endites brown, lighter toward prolateral edge. Labium brown, lighter anteriorly. Sternum yellow. Abdomen yellow with no markings. First legs yellow; femora dark brown laterally and ventrally with scattered white scales and dorsal yellow stripe. Other segments darker ventrally, lighter dorsally. Other legs yellow. Pedipalps brown mottled with yellow, tips yellow.

Female.—Total length 3.30-4.00. Carapace 1.36-1.50 long, 1.13-1.20 wide, 0.57-0.62 high at PLE. Ocular area 0.60-0.66 long, 0.82-0.90 wide anteriorly and 0.90-0.98 wide posteriorly. Chelicerae 0.35-0.45 long 0.24-0.35 wide (four females from Sonora, Mexico). PME closer to ALE than to PLE. Leg formula 1432. Carapace orange, black around eyes, lighter laterally. Clypeus with white hairs. Chelicerae red-brown. Endites and labium red brown. Sternum yellow-brown. Abdomen yellow, occasionally with faint central stripe. All legs yellow-brown. Pedipalpi yellow with proximal dorsal dark spots on all segments.

Distribution.—Known only from Sonora, Mexico (Map 1).

Natural history.—Males collected in April and July, females in March and August.

Specimens examined.—MEXICO: SONORA; Guaymas (AMNH, MCZ), 4-8 mi. S Peon (FSCA), 6 mi. N San Carlos Bay (UCB).

Hentzia chekika, new species

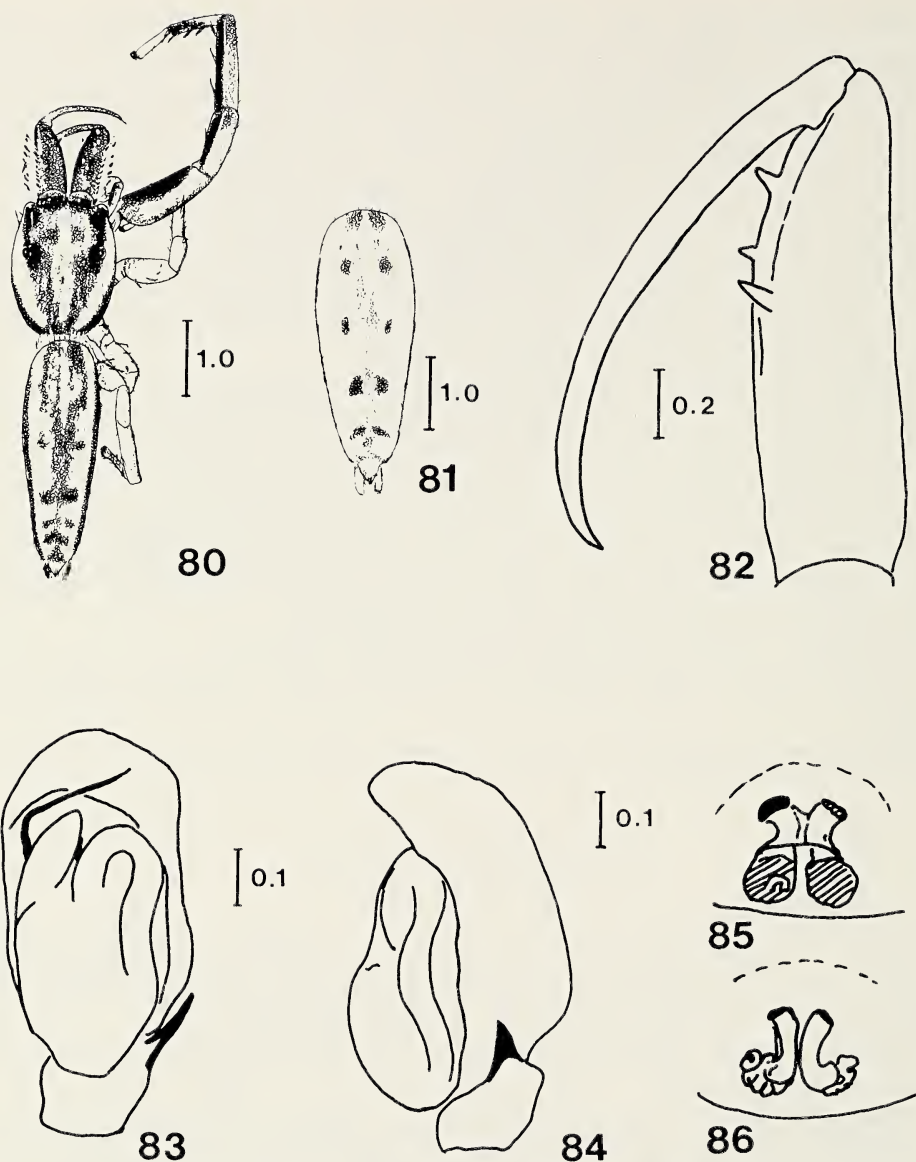
Figs. 80-86, Map 6

Types.—Male holotype and female allotype from Matheson Hammock Park, Miami, Dade Co., Florida (7 May 1985; G. B. Edwards), deposited in the FSCA. Male and female paratypes in the FSCA, AMNH and MCZ.

Etymology.—The specific name refers to one of the last chiefs of the Calusa Indians of south Florida.

Diagnosis.—*Hentzia chekika* is one of the largest of the *Hentzia* species; members of both sexes usually being over 5 mm in length. Males resemble those of *H. grenada*, but are larger, lack the loop on the retromargin of the palpal bulb (Figs. 83, 84), have a distinctive pattern of elongated spots connected with a central tree-like marking on the dorsal abdomen (Fig. 80), and the epigynum has longer J-shaped ducts than *H. poenitens*, but much shorter than those of *H. grenada* (Fig. 86).

Male.—Total length 4.35-6.30. Carapace 1.70-2.30 long, 1.25-1.80 wide, 0.65-1.00 high at PLE. Ocular area 0.70-1.05 long, 1.10-1.45 wide anteriorly and 1.05-1.45 wide posteriorly. Chelicerae 0.70-2.00 long, 0.33-0.50 wide (10 males from Dade Co., Florida, and 1 male from Cuba). PME closer to ALE than to PLE. Leg formula 1423. Carapace yellow-brown with red-brown bands on either side. Dorsum with narrowing central band of white hairs nearly reaching AME. White spots of hairs between anterior eyes; otherwise black around eyes except brown around AME. Lateral white bands followed by black margin around carapace.



Figures 80-86.—*Hentzia chekika* n. sp.: 80-84, from Dade Co., Fla., 80, male, dorsal view; 81, female, dorsal view of abdomen; 82, left chelicera of male, ventral view; 83, 84, palp of male; 83, ventral view; 84, retrolateral view; 85, 86, epigynum of female from Soledad, Cuba; 85, ventral view; 86, dorsal view.

Clypeus covered with white hairs. Chelicerae red to yellow brown, iridescent, often darker prolaterally. Fang of holotype with distal 1/4 lighter. Endites brown, holotype with light prolateral 1/2. Labium brown. Sternum orange. Abdomen yellow-brown with distinctive darker pattern (Fig. 80). Venter yellow. First legs yellow-brown, dark brown anteroventrally except tarsi and metatarsi. Metatarsi brown, darker distally. Tarsi yellow. Other legs yellow. Pedipalpi yellow; bulb brown and proximal brown bands on patellae and tibiae.

Female.—Total length 4.60-7.00. Carapace 1.90-2.40 long, 1.35-1.80 wide, 0.65-0.90 mm high. Ocular area 0.85-1.00 long, 1.20-1.40 wide anteriorly, 1.20-1.40



Map 6.—West Indies and Florida, showing distribution of *Hentzia chekika* (closed circles), *H. zombia* (open circles), and *H. footei* (closed squares).

wide posteriorly. Chelicerae 0.50-0.80 long, 0.40-0.50 wide (11 females from Dade Co., Florida, and 6 from Cuba). PME closer to ALE than to PLE. Leg formula 1423. Carapace orange with brown lateral area, followed by orange and then a black margin. White hairs scattered throughout. Black around eyes except brown around AME. Clypeus covered with white hairs. Chelicerae red-brown. Endites red-brown, lighter medially. Labium red-brown, lighter anteriorly. Sternum orange to yellow with dark lateral bands in allotype. Abdomen yellow with brown pattern (Fig. 71). Venter yellowish. First legs orange with brown prolateral femora and patellae, dark brown distal band on tibiae and metatarsi, white scales on proventral femora. Other legs yellow to orange. Pedipalpi yellow-orange with dark dorsal bands on proximal tibiae, patellae and tarsi.

Distribution.—Florida, Bahamas and Cuba (Map 6).

Natural history.—Males have been collected from March to May, July to September, November to December. Females from January, March, May to August and November. Probably both sexes can be collected in any month of the year. Records which include habitat data indicate that this species is found primarily on tall feather palms such as *Cocos nucifera* and *Roystonea regia*.

Specimens examined.—**BAHAMAS:** Abaco Cays (AMNH), Andros (AMNH), Freeport (AMNH), Grand Bahama (AMNH), North Bimini (AMNH), Stirrup Cay (FSCA). **CUBA:** Soledad (MCZ), Cienaga de Zapata (MCZ). **U.S.A.:** **FLORIDA:** Broward Co., Ft. Lauderdale (FSCA); Dade Co., Miami-Doral Country Club (FSCA), Matheson Hammock (FSCA), Kendall (AMNH), Crandon Park (AMNH), Perrine (AMNH); Lee Co., Sanibel Island (MCZ). **Monroe Co.,** Flamingo (FSCA).

VERNALIS SPECIES GROUP

This group takes the name of its most aberrant member by virtue of priority. *Hentzia vernalis* appears to have been derived from *footei*-like ancestors, based on the structure of the male palpi and chelicerae (Figs. 89-92, 96-99). All members of this species group have truncated retromarginal teeth in the male which distinguishes them from all other species in the genus (Figs. 89, 90, 96, 97, 104, 109). Most large males in this species group, with the possible exception of *H. footei*, have very elongate chelicerae. The four species in this group, *H. vernalis*, *H. footei*, *H. antillana* and *H. whitcombi* (n. sp.) range from Cuba to Colombia. The two species pairs within the species group (Fig. 15) can be separated by the structure of the retromarginal teeth of the males. Both *H. vernalis* and *H. footei* have relatively short, straight, truncated or (rarely) bifurcate retromarginal teeth (Figs. 89, 90 and 96, 97), whereas *H. antillana* and *H. whitcombi* have angled and truncate retromarginal teeth (Figs. 104, 109). The species can be further divided by the structure of the epigyna and arrangement of cheliceral teeth.

Hentzia vernalis (Peckham and Peckham)

Figs. 87-94, Map 4

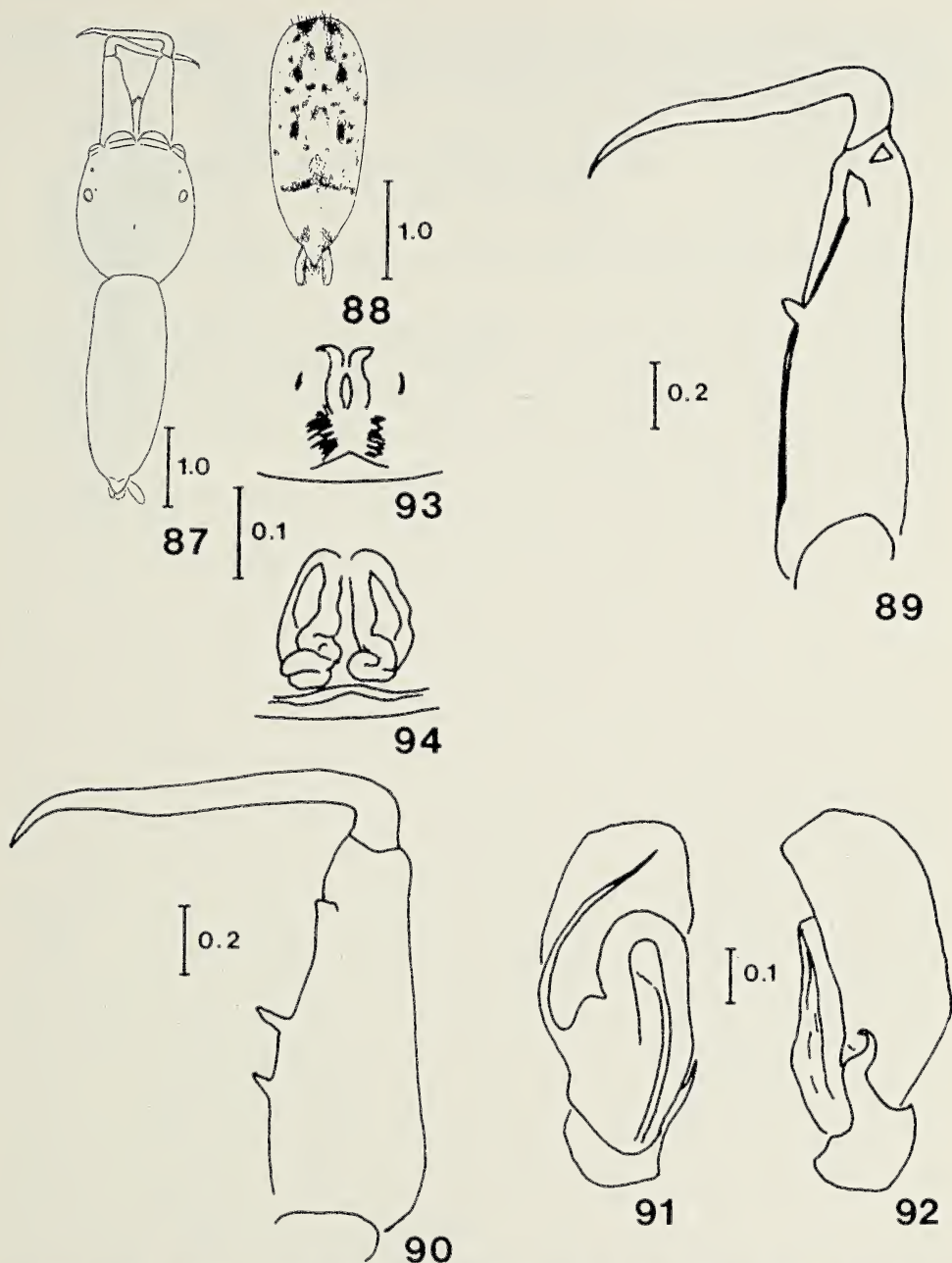
Anoka vernalis Peckham and Peckham 1893:701 (holotype male from St. Vincent in the MCZ examined).

H. vernalis Roewer 1954:1218.

Diagnosis.—Males are unlike any other *Hentzia* in the structure of their chelicerae (Figs. 89, 90) and their palpi (Figs. 91, 92). They appear to form the most extreme end of the spectrum for their species group. The females have hair pencils like other *Hentzia*, but the epigynum is unlike any other member of the genus in that there appears to be two tubes on either side (Figs. 93, 94).

Male.—Total length 3.75-4.85. Carapace 1.55-2.00 long, 1.20-1.50 wide, 0.65-0.80 high at PLE. Ocular area 0.70-0.80 long, 1.05-1.25 wide anteriorly, 1.08-1.30 wide posteriorly. Chelicerae 0.85-1.50 long, 0.35-0.46 wide (7 males from St. Vincent, Trinidad, Grenada and Barbados). PME closer to ALE than to PLE. Leg formula 1423. Carapace orange, ocular area yellow with lateral white areas from posterior to eyes. Eyes surrounded by black, except AME red-brown. Clypeus covered with white hairs. Chelicerae orange. Endites, labium and sternum flesh-colored. Abdomen yellow with four vague darker spots. Venter yellow with two parallel darker lines. First legs orange. Other legs yellow. Pedipalpi yellow.

Female.—Total length 3.50-5.50. Carapace 1.40-1.90 long, 1.10-1.50 wide, 0.55-0.70 high at PLE. Ocular area 0.60-0.85 long, 0.95-1.20 wide anteriorly and 1.00-1.30 wide posteriorly. Chelicerae 0.30-0.60 long, 0.25-0.50 wide (six females from St. Vincent and Grenada). AME equidistant between ALE and PLE. Leg formula 1432. Carapace orange, black around eyes except brown around AME. Darker around lateral areas of carapace and dorsally to midline. Clypeus covered with white hairs. Chelicerae, endites and labium orange. Sternum yellow. Abdomen yellow with pattern of speckles followed by band 3/4 way to spinnerets, similar to that found on many *H. antillana* females. First legs yellow, slightly darker dorsally on distal patellae and tibiae. Other legs and pedipalpi yellow.



Figures 87-94.—*Hentzia vernalis* (Peckham and Peckham): 87, 89, 91-94, from St. Vincent; 87, holotype male, dorsal outline view; 88, female, dorsal view of abdomen; 89, left chelicera of holotype male, ventral view; 90, left chelicera of male from Barbados, ventral view; 91, 92, palp of holotype male; 91, ventral view; 92, retrolateral view; 93, 94, epigynum of female; 93, ventral view; 94, dorsal view.

Distribution.—Northern South America, Trinidad, Barbados, St. Vincent and Grenada (Map 4).

Natural history.—Males collected in April and August-September (Other specimens with no dates). Females in February and August-October. Probably found as adults all year.

Specimens examined.—**BARBADOS:** Barbados (USNMNH), Bridgetown (AMNH). **COLOMBIA:** Cienaga (FSCA), Mag. Tasajera (FSCA). **GRENADA:** Broadway (MCZ), St. Georges (AMNH). **ST. VINCENT:** Island record (MCZ), Kingston (AMNH). **TRINIDAD:** Port-of-Spain (MCZ).

Hentzia footei (Petrunkevitch)

Figs. 95-101, Map 6

Wala footei Petrunkevitch 1914:330 (holotype male from Dominica in AMNH examined).
H. footei Roewer 1954:1217.

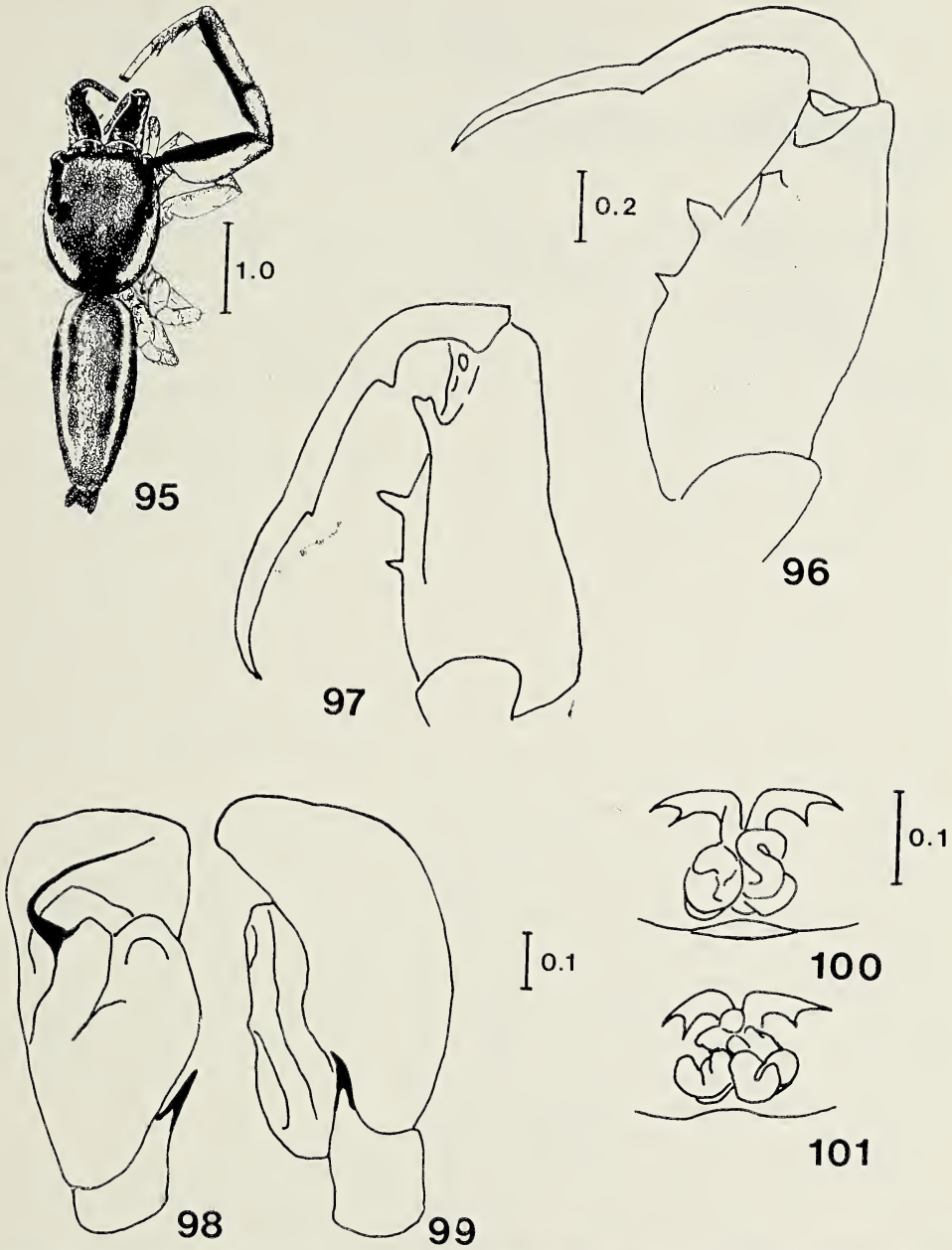
Diagnosis.—Males differ from all other *Hentzia* in having at least one tooth on the fang, and occasionally having a bifurcate retromarginal tooth (Figs. 96, 97). The female epigynal structure (Figs. 100, 101) differs from other *Hentzia* in having slender downturned tubes and deeply indented openings. In this character the epigynum is similar to that of *Anicius dolius*.

Male.—Total length 2.90-4.43. Carapace 1.30-1.89 long, 1.05-1.48 wide, 0.55-0.82 high at PLE. Ocular area 0.65-0.90 long, 0.93-1.23 wide anteriorly and 0.93-1.31 wide posteriorly. Chelicerae 0.42-1.07 long, 0.25-0.49 wide (10 males from Dominica, Martinique and St. Lucia). PME closer to ALE than to PLE. Leg formula 1423. Carapace red-brown; lighter scales and white band of hairs laterally. Black around eyes and margin. Clypeus dark brown. Chelicerae yellow to red-brown. Endites gray to dark brown with prolateral distal 1/3 cream. Labium dark brown with distal 1/6 cream. Sternum yellowish. Abdomen yellow-brown, slightly metallic, with indistinct cross bands (especially just anterior from spinnerets). Lateral dorsal white bands, followed by gray toward venter. Venter brown with two narrow posterior gray stripes. First legs yellow to red-brown with 1/2 prolateral and ventral femora, patellae and tibiae dark brown and proximal and distal patellae and tibiae dark brown. Tarsi sometimes with yellow tip. Holotype with only indistinct markings on first legs. Other legs yellow. Pedipalpi yellow with orange bulb with dark band or streak on distal femora.

Female.—Total length 4.70-5.05. Carapace 1.90-2.15 long, 1.48-1.68 wide, 0.75-0.80 high at PLE. Ocular area 0.85-0.90 long, 1.30-1.40 wide anteriorly and 1.30-1.45 side posteriorly. Chelicerae 0.50-0.60 long, 0.40-0.45 wide (three females from St. Lucia). PME closer to ALE than to PLE. Leg formula 1432. Carapace orange-brown. Black around eyes, except brown around AME. Clypeus covered with white hairs. Chelicerae orange brown. Endites red-brown with lighter prolateral anterior edge. Labium red-brown with lighter anterior 1/5. Sternum yellow. Abdomen yellow with brown central pattern. Anteriorly there is a yellow streak ending in a claw-like mark on the midline followed by a dark brown inverted V and three connected triangle decreasing in size ending at the spinnerets. Lateral to these markings the abdomen is spotted and blotched with brown. Venter yellow with dark triangular marking anterior to the spinnerets and black ring around spinnerets. First legs yellow-brown; prolateral brown bands on distal femora, patellae, tibiae and metatarsi, and proximal tibiae. Other legs yellow. Pedipalpi yellow.

Distribution.—Dominica, Martinique and St. Lucia in the southern Lesser Antilles (Map 6).

Natural history.—Males from January, June-July and October. Females from October. Probably found as adults all year.



Figures 95-101.—*Hentzia footei* (Petrunkévitch): 95, male from St. Lucia, dorsal view; 96, 97, left chelicerae of males; 96, holotype from Dominica, ventral view; 97, Martinique, ventral view; 98, 99, palp of holotype male from Dominica; 98, ventral view; 99, retrolateral view; 100, 101, epigynum of female from St. Lucia; 100, ventral view; 101, dorsal view.

Specimens examined.—**BRITISH WEST INDIES:** St. Lucia (MCZ). **DOMINICA:** Roseau (AMNH), Springfield (USNMNH). **MARTINIQUE:** Fond la Haye (AMNH), Pointe Ferret (AMNH).

Hentzia antillana Bryant

Figs. 102-108, Map 3

Wala vernalis Petrunkevitch 1930:139 (misidentification).*Hentzia antillana* Bryant 1940:494 (holotype male and allotype female from Antigua in MCZ examined).

Diagnosis.—Males can be distinguished from all other members of the genus except *H. whitcombi* n. sp. and some specimens of *H. footei* by the presence of a curved, truncated retromarginal tooth on the chelicerae. It can be distinguished from *H. whitcombi* by the pattern of promarginal teeth in relationship to the retromarginal tooth and from *H. footei* by the general structure of the chelicerae (Fig. 104). The female epigynal structure has characteristic trumpet-shaped tubes leading to the spermathecae (Fig. 108).

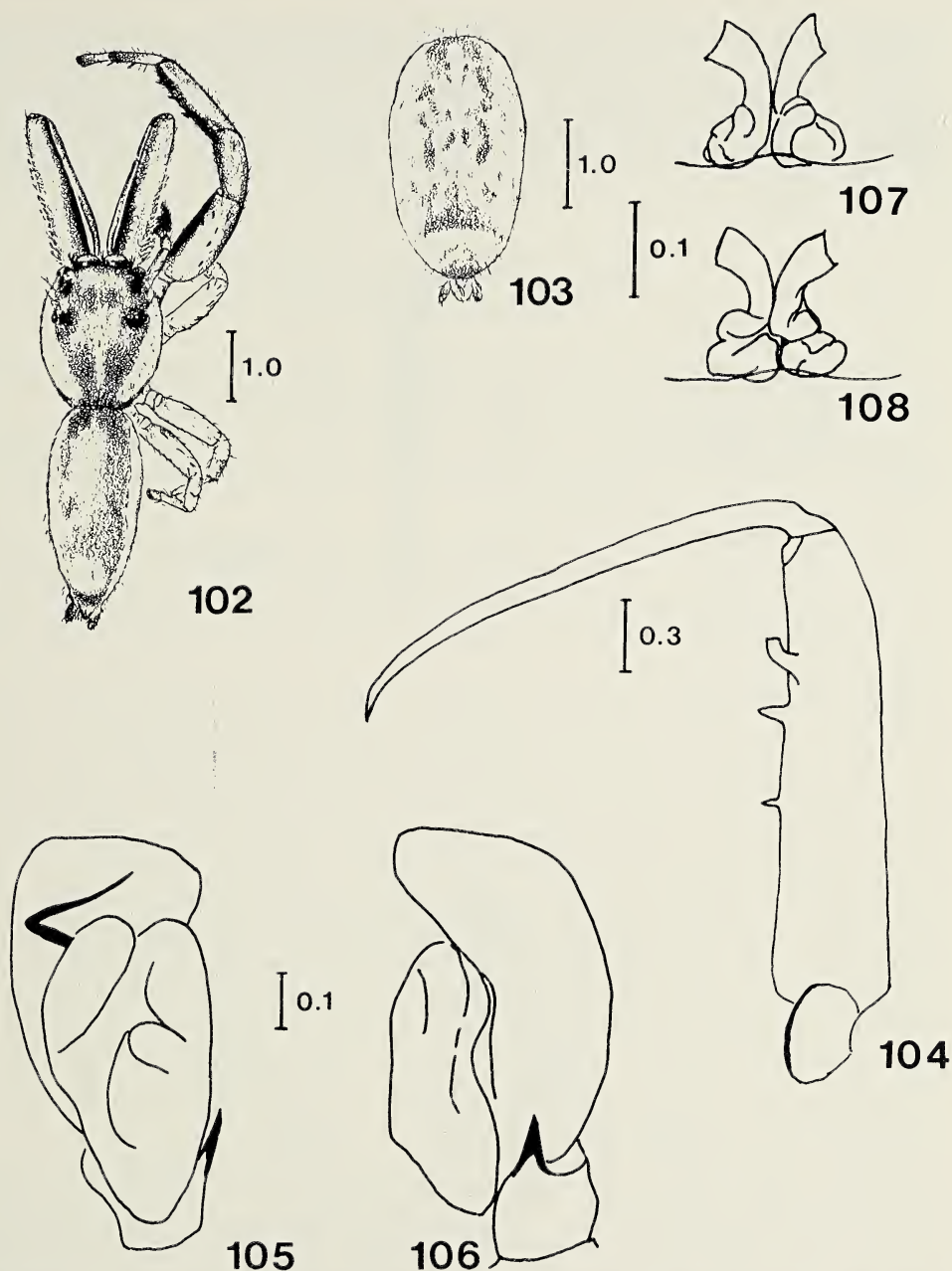
Male.—Total length 3.60-5.00. Carapace 1.50-2.00 long, 1.30-1.70 wide, 0.70-1.00 high at PLE. Ocular area 0.70-0.90 long, 1.00-1.25 wide anteriorly, 1.15-1.40 wide posteriorly. Chelicerae 1.10-2.00 long, 0.30-0.43 wide (10 males from Virgin Gorda, British Virgin Islands). PME slightly closer to ALE than to PLE. Leg formula 1423. Carapace red-brown with white hairs laterally. Dark around eyes. Clypeus with white hairs. Chelicerae yellow brown, promargin red-brown; fang darker. Endites red-brown with lighter inner edge. Labium dark brown. Sternum yellow-brown. Abdomen golden brown, slightly metallic. Venter and lateral areas yellow-gray. First legs yellow-brown; darker under prolateral femora, patellae and tibiae. Indistinct bands on distal patellae, tibiae and metatarsi. Other legs yellow. Pedipalpi red-brown; cymbium and bulb darker.

Female.—Total length 4.05-5.50. Carapace 1.50-2.10 long, 1.25-1.70 wide, 0.60-0.90 high at PLE. Ocular area 0.70-0.80 long, 1.00-1.30 wide anteriorly and 1.10-1.45 wide posteriorly. Chelicerae 0.45-0.80 long, 0.30-0.50 wide (10 females from Virgin Gorda, British Virgin Islands). PME closer to ALE than to PLE. Leg formula 1423. Carapace red-brown with lateral white hairs. Eyes dark. Clypeus with white hairs. Chelicerae red-brown. Endites red-brown with yellow prolateral tip. Labium red-brown. Sternum yellow-brown. Abdomen yellow with red-brown markings. A posterior dark band (also seen in *H. vernalis* and *H. squamata* females) is almost always present. First legs red-brown. Other legs yellow. Pedipalpi yellow; annulate at proximal joints.

Distribution.—West Indies from Dominica to Cuba (Map 3).

Natural history.—Males and females have been collected in every month but December. It is probably found in all months as adults. In Puerto Rico the species was common in citrus groves in May and was also occasionally swept from tall grass. In Guadeloupe they were abundant in citrus in February. It is sympatric with *H. whitcombi* over much of its range.

Specimens examined.—**ANTIGUA:** Antigua (MCZ, USNMNH), Crosbies (MCZ), St. Johns (AMNH), Shirley Heights (MCZ). **BARBUDA:** Codrington (AMNH). **BRITISH VIRGIN ISLANDS:** Amegada (AMNH, USNMNH), Beef Island (AMNH), George Dog Island (AMNH), Ginger Island (AMNH), Greater Thatch Island (AMNH), Green Cay (AMNH), Guana Island (AMNH, USNMNH), Little Comonoe (AMNH), Little Thatch Island (AMNH), Little Tobago (AMNH), Sandy Key (AMNH), Tortola (AMNH, MCZ, USNMNH), Virgin Gorda (AMNH, MCZ). **BRITISH WEST INDIES:** St. Kitts (MCZ), St. Lucia (MCZ), St. Nevis (MCZ). **CUBA:** Ceiba (AMNH). **DOMINICA:** country record (MCZ), Fond Sophie (AMNH), Roseau (AMNH); **GUADELOUPE:** Maire Galant (FSCA), Petit Bourg (FSCA), Pointe-a-Pitre (AMNH). **HAITI:** Port-au-Prince (MCZ). **LEEWARD ISLANDS:** Saint Maarten (AMNH), Saba (MCZ). **MARTINIQUE:**



Figures 102-108.—*Hentzia antillana* Bryant: 102, 103, from Isabela, Puerto Rico; 102, male, dorsal view; 103, female, dorsal view of abdomen; 104-106, holotype male from Antigua; 104, left chelicera, ventral view; 105, 106, palp; 105, ventral view; 106, retrolateral view; 107, 108, epigynum of female from Virgin Gorda, British Virgin Islands; 107, ventral view; 108, dorsal view.

Fond la Haye (AMNH), Pointe Ferret (AMNH) Trois Ilets (AMNH). **MONTSEERRAT:** Plymouth (AMNH). **PUERTO RICO:** Aibonito (AMNH), Arecibo (AMNH), Barros (AMNH), Blanquilla (AMNH), Cabeza de Parro Island (AMNH), Cambalache Forest (AMNH), Camuy (AMNH), Caña Gorda (DBR), Cayo Ahogado (AMNH), Cayo Caracoles (AMNH), Cayo San Cristobal (AMNH), Chicken Island (AMNH), Coamo Springs (AMNH), Corozal (AMNH), Desecheo Island (AMNH), Isabela (DBR), Isla Palominires (MCZ), Isla Ramos (AMNH), Isleta Marina (AMNH), Laguna

Cartegena (MCZ), La Parquera (MCZ), Loma Tinaja (AMNH), Luquillo Mountains (MCZ), Manati (AMNH), Maricao Bosque National (MCZ), Mayaguez (AMNH, DBR, MCZ), Muertes Island (AMNH), Nicacos Island (MCZ), Quebradilla (AMNH), Pico Atalaya (AMNH), Pineros Island (AMNH), Ratones Island (AMNH), Rio Piedras (MCZ), San Juan (AMNH, MCZ), Vega Baja (AMNH), Vivevero de Catalina (AMNH). UNITED STATES VIRGIN ISLANDS: Anegada (AMNH), Hassel Is. (AMNH), St. Croix (MCZ, USNMNH), St. John (FSCA, MCZ, USNMNH), St. Thomas (MCZ).

Hentzia whitcombi, new species

Figs. 109-113, Map 5

Types.—Holotype male and allotype female from Petit Bourg, Basse Terre, Guadeloupe (25 February 1977. W. H. Whitcomb) deposited in the FSCA.

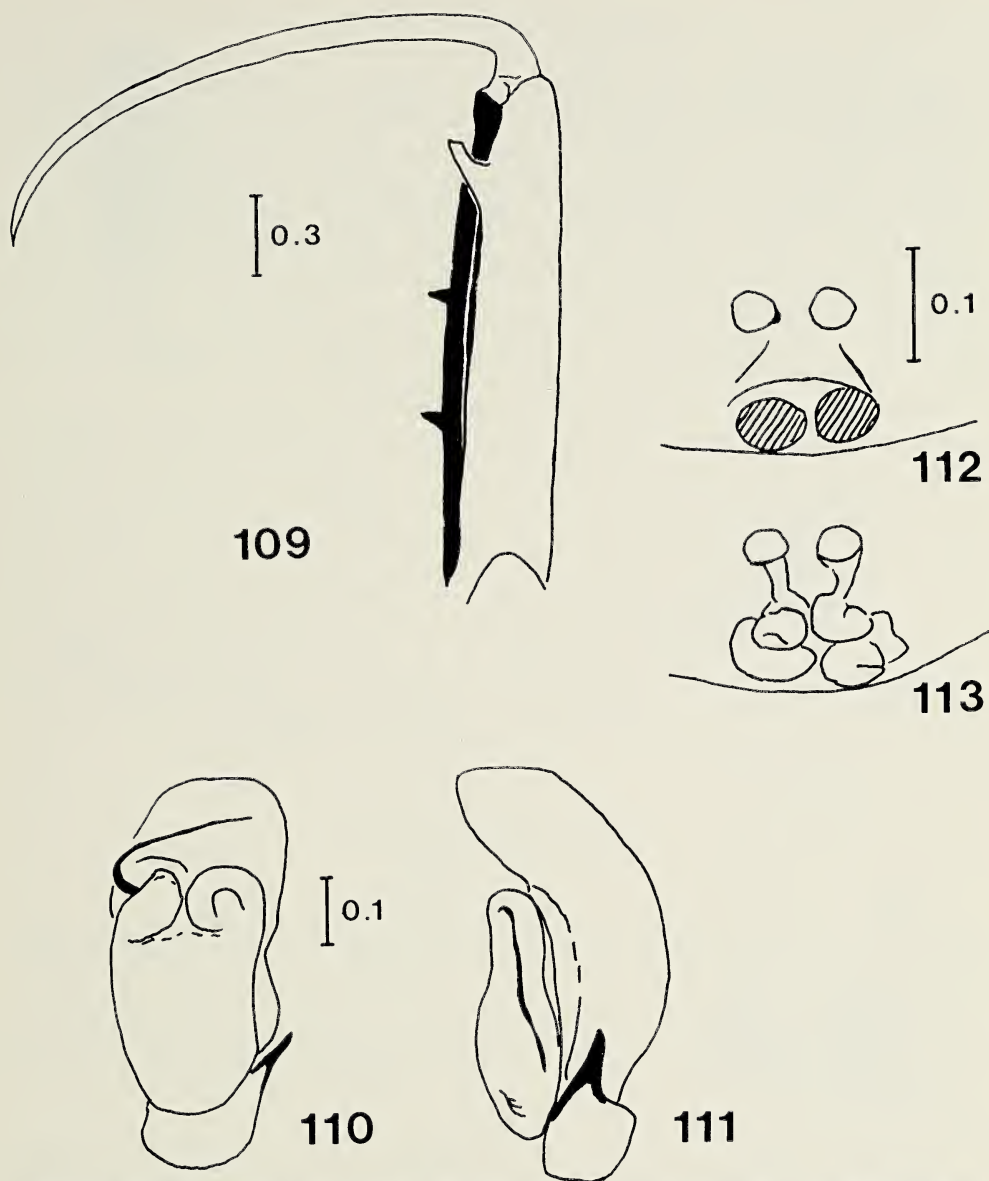
Etymology.—The species is named for Dr. W. H. Whitcomb, Professor Emeritus, University of Florida, who collected the type series during his study on the natural enemies of citrus pests.

Diagnosis.—Males differ from all other *Hentzia* except *H. antillana* in having long chelicerae with a curved truncated retromarginal tooth. They differ from *H. antillana* males in the arrangement of the cheliceral teeth (Fig. 109). The female epigynum differs from that of *H. antillana* by having round openings (Figs. 112, 113).

Males.—Total length 3.20-4.90. Carapace 1.50-1.90 long, 1.20-1.50 wide, 6.50-8.50 high at PLE. Ocular area 0.70-0.92 long, 1.00-1.22 wide anteriorly and 1.00-1.28 wide posteriorly. Chelicerae 0.65-1.70 long, 2.40-4.00 wide (10 males from Guadeloupe). PME closer to ALE than to PLE. Leg formula 1423. Carapace red-brown with central dorsal spearhead-like light marking with point toward posterior. Lateral areas with white scales. Black around eyes except dark brown around AME. Carapace with scattered iridescent scales. Clypeus brown with white hairs. Chelicerae red brown, darker prolaterally, with fringe of white hairs. Distal 1/5 of fang yellowish. Endites dark brown, tip pale. Labium dark brown, tip pale. Sternum orange. Abdomen dark brown with darker markings, similar to those of *H. antillana*. Dorsum with iridescent scales. Lateral area with pattern of white and brown stripes. Venter light brown. First legs yellow; dark brown prolaterally and ventrally. Other legs yellow. All legs with iridescent scales. Pedipalpi yellow; bulb and cymbium brown.

Female.—Total length 3.80-5.40. Carapace 1.70-2.00 long, 1.30-1.60 wide, 0.70-0.80 high at PLE. Ocular area 0.70-0.85 long, 1.15-1.30 wide anteriorly and 1.20-1.40 wide posteriorly. Chelicerae 0.40-0.60 long, 0.30-0.45 wide (10 females from Guadeloupe). PME closer to ALE than to PLE. Leg formula 1423. Carapace orange; white scales laterally. Black around eyes except brown around AME. Clypeus with white hairs. Chelicerae orange-brown. Endites dark brown, prolateral tip pale. Labium dark brown with pale tip. Sternum yellow. Abdomen yellow with brown markings like *H. antillana*. Venter yellow. First legs yellow with light brown markings on prolateral distal femora, patellae and tibiae, and retrolateral femora. Other legs yellow. Pedipalpi yellow with brown dorsal proximal markings on patellae, tibiae and tarsi.

Natural history.—Males have been collected in January-April and June-July. Females have been collected from January-March and May-August. They probably occur throughout the year.



Figures 109-113.—*Hentzia whitcombi* n. sp. from Basse Terre, Guadeloupe: 109, left chelicera of male, ventral view; 110, 111, palp of male; 110, ventral view; 111, retrolateral view; 112, 113, epigynum of female; 112, ventral view; 113, dorsal view.

Specimens examined.—**BRITISH VIRGIN ISLANDS:** Peter Island (AMNH). **BRITISH WEST INDIES:** St. Kitts (MCZ). **DOMINICA:** Portsmouth (AMNH), Roseau (USNMNH). **GUADELOUPE:** Pointe-a-Pitre (AMNH), Petit Bourg (FSCA), Lamentin (FSCA). **MONTSERRAT:** Galways Estate (AMNH). **PUERTO RICO:** Aguadilla (USNMNH), Culebrita Island (AMNH), La Pauquera (MCZ), Levin's Rock (AMNH), Maricao (MCZ), Maracao National Forest (AMNH), Mayaguez (AMNH, MCZ), Rio Piedras (AMNH), Toro Negro (MCZ). **UNITED STATES VIRGIN ISLANDS:** St. John (FSCA), St. Thomas (MCZ).

VITTATA SPECIES GROUP

This group contains two species formerly placed in the genera *Parahentzia* Bryant and *Maeviobeata* Caporiacco. It also contains the *Hentzia* or *Wala* species *squamata* and *vittata*, as well as two new species, *calypso* and *zombia*, for a total of six species. All the known males have characteristic cheliceral teeth, with a spike-like retromarginal tooth and usually two smaller promarginal teeth (Figs. 115, 116, 125, 132, 139, 148, 149). Most males in this species group have robust chelicerae and are less elongate than other *Hentzia* species. *Hentzia calypso* is one of the smallest species of the genus, but the rest are larger and comparable to most other *Hentzia* species in size. The species range from the Bahamas and Cuba to northern South America and Central America.

The *vittata* group part of the cladogram (Fig. 15) is more or less arbitrary in that *H. zombia* is known only from females, *H. squamata* is somewhat aberrant in that it has males with long chelicerae, and *H. calypso* is more elongate and much smaller than other species in the group. In addition, *H. mandibularis* males often have a strange tubercle on the dorsal chelicerae. The only two species that can be easily related, other than by the characters found in the group as a whole, are *H. vittata* and *H. parallela*. The males of these are difficult to separate and it is possible that they represent variations of one widespread species. At present I am treating them as separate species, but I would not be totally surprised if they turned out to be synonyms, although the females seem to exhibit some differences that may separate these similar species (see species descriptions).

Hentzia vittata (Keyserling)

Figs. 114-122, Map 7

Icius vittatus Keyserling 1885:504 (holotype female from "United States" in MCZ examined).

Wala albovittata Keyserling 1885:517 (holotype male from "United States" in MCZ examined). NEW SYNONYMY.

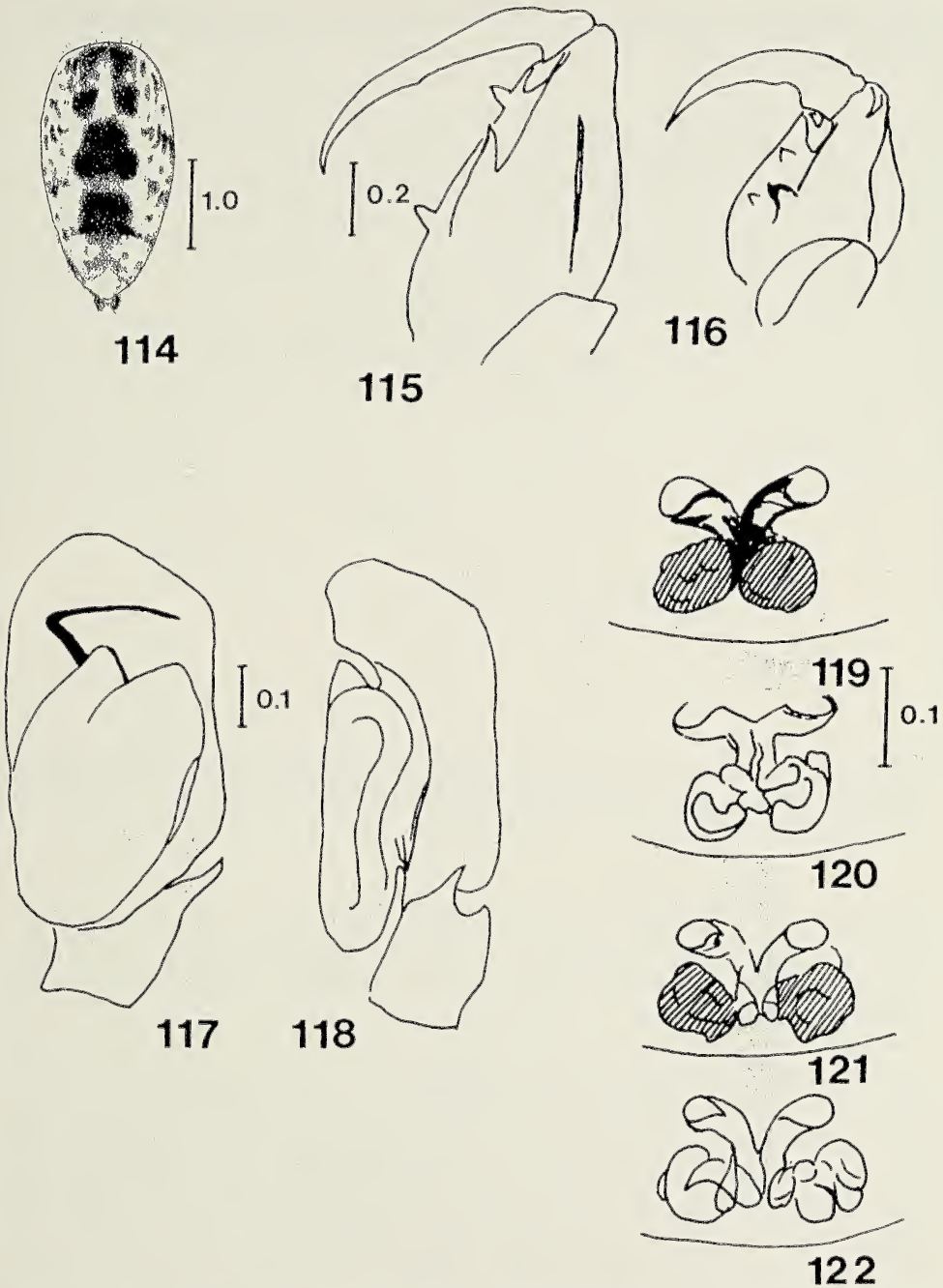
Anoka peckhami Cockerell 1893:221 (holotype and paratypes from Jamaica in MCZ examined). NEW SYNONYMY.

Anoka moneagua Peckham and Peckham 1894:127 (holotype and paratypes in MCZ examined). NEW SYNONYMY.

Hentzia peckhami Bryant 1943:488. NEW SYNONYMY.

Diagnosis.—Males differ from all other *Hentzia* males except for *H. parallela* and *H. calypso* in the structure of the chelicerae (Figs. 115, 116). They differ from *H. calypso* in size and pattern. *H. vittata* and *H. parallela* are very close and can be distinguished primarily by the female epigyna of *H. vittata* (Figs. 119-122), which have wider spermathecal areas than either *H. parallela* or *H. calypso*.

Male.—Total length 2.95-5.17. Carapace 1.39-2.21 long, 1.23-1.80 wide, 0.66-1.15 high at PLE. Ocular area 0.66-0.90 long, 1.07-1.31 wide anteriorly, 1.15-1.48 wide posteriorly. Chelicerae 0.41-1.23 long, 0.37-0.51 wide (11 males from Jamaica plus the holotype of *Wala albovittata* from "United States"). PME closer to ALE than to PLE. Leg formula 1423. Carapace red-brown; white hairs laterally. Eyes surrounded by black except brown around AME. Clypeus covered with white hairs. Chelicerae red-brown, metallic. Endites and labium dark red-brown, sometimes with lighter tips. Sternum light red-brown to orange. Abdomen orange to golden brown, often with slight indication of markings dorsally and



Figures 114-122—*Hentzia vittata* (Kerserling): 114, female from Torrington, Jamaica, dorsal view of abdomen; 115, left chelicera of male (holotype of *Anoka peckhami* Cockerell) from Jamaica, ventral view; 116, left chelicera of male from Freeport, Grand Bahama, ventral view; 117, 118, palp of male (holotype of *Anoka moneagua* Peckham and Peckham) from Moneague, Jamaica; 117 ventral view; 118, retrolateral view; 119-122, epigyna of females; 119, 120, from Jamaica; 119, ventral view; 120, dorsal view; 121, 122, from Cuba; 121, ventral view; 122, dorsal view.



Map 7.—West Indies and Central America, showing distribution of *Hentzia vittata* (closed circles) and *H. parallela* (closed squares).

sometimes with lateral lighter bands. Lateral area darker; venter gray-brown to brown. First legs red-brown, darker ventrally and laterally. Tarsus orange. Other legs yellow-brown to yellow. Coxae yellow. Pedipalpi red-brown, femora and patellae sometimes yellow.

Female.—Total length 3.44-5.00. Carapace 1.48-1.89 long, 1.23-1.72 wide, 0.65-0.82 high at PLE. Ocular area 0.74-0.98 long, 0.98-1.30 wide anteriorly and 1.15-1.39 wide posteriorly. Chelicerae 0.40-0.57 long, 0.30-0.41 wide (10 females from Jamaica, Haiti and the holotype of *Icius vittatus* from "United States"). PME closer to ALE than to PLE. Leg formula 1432. Carapace yellow to orange-brown with lateral white hairs. Eyes surrounded by black, except brown around AME. Glypeus white to yellow. Chelicerae light red-brown to orange. Endites and labium red-brown to orange, lighter distally. Sternum red-brown to yellow-brown. Abdomen yellow with either four dark brown spots dorsally followed by a dark cross-band or with a pattern of two brown spots anteriorly, followed posteriorly by two to three triangular to square markings, ending at spinnerets. Venter yellow to yellow brown. First legs yellow-brown to orange. Other legs yellow to yellow-brown. Pedipalpi yellow with darker proximal dorsal spots on all but femora.

Distribution.—Bahamas, Cuba, Hispaniola and Jamaica (Map 7).

Natural history.—Males have been collected in January, March-April, June-July and October-December. Females in January-June and August-December. Adults are present throughout the year.

Specimens examined.—**BAHAMAS:** Abaco Cays (AMNH), Andros (AMNH), Cat Island (AMNH), Elbow Cay (AMNH), Grand Bahama (AMNH), Great Exuma (MCZ), Harbor Island (MCZ), Little Harbor Cay (AMNH), Lucaya (AMNH), Nassau (AMNH), New Providence Island (AMNH), North Bimini (AMNH), South Bimini (AMNH), Stirrup Cay (FSCA), West Caicos (AMNH). **CUBA:** Buenos Aires (MCZ), San Blas (MCZ), Soledad (MCZ), 7 km N Vinales (AMNH). **DOMINICAN REPUBLIC:** Bara Hora (MCZ), Boca Caica (AMNH), La Matica (AMNH), Largo Enriquillo (FSCA), La Vega (MCZ), Las Waitas (MCZ), Nisibon (FSCA), Puerto Plata (MCZ), Santo Domingo (AMNH), S of Santiago (MCZ). **HAITI:** Carrefour (AMNH), Diguini (MCZ), Formond (FSCA), Grand Anne (MCZ), Grand Riviere (MCZ), Kenscoff (AMNH), La Boule (AMNH), La Hoatte (MCZ), Les Anglais (FSCA), Port-au-Prince (AMNH, MCZ), Post Terre Rouge (MCZ). **JAMAICA:** Christina (AMNH, MCZ), Discovery Bay (AMNH), The Great Morass (AMNH), Hanover Askenish (MCZ), Holland Bay (AMNH), James (MCZ), Kingston (AMNH, MCZ), Manderville (MCZ), Moneague (MCZ), 2.5 mi. E Ocho Rios (MCZ), Port Antonis (MCZ), Port Henderson (MCZ), Portland (MCZ), Robin's Bay (MCZ), Roundhill (AMNH), St. Andrew (MCZ), St. Ann (MCZ), St. Catherine (MCZ), St. Elizabeth (MCZ), St. Mary (MCZ), St. Thomas (MCZ), Unity Valley (AMNH), Westmoreland (MCZ), Whitehouse (AMNH).

Hentzia parallela (Peckham and Peckham)

Figs. 123-129, Map 7

Anoka parallela Peckham and Peckham 1894:129 (holotype male from Trinidad in MCZ examined).

Wala parallela Petrunkevitch 1911:717.

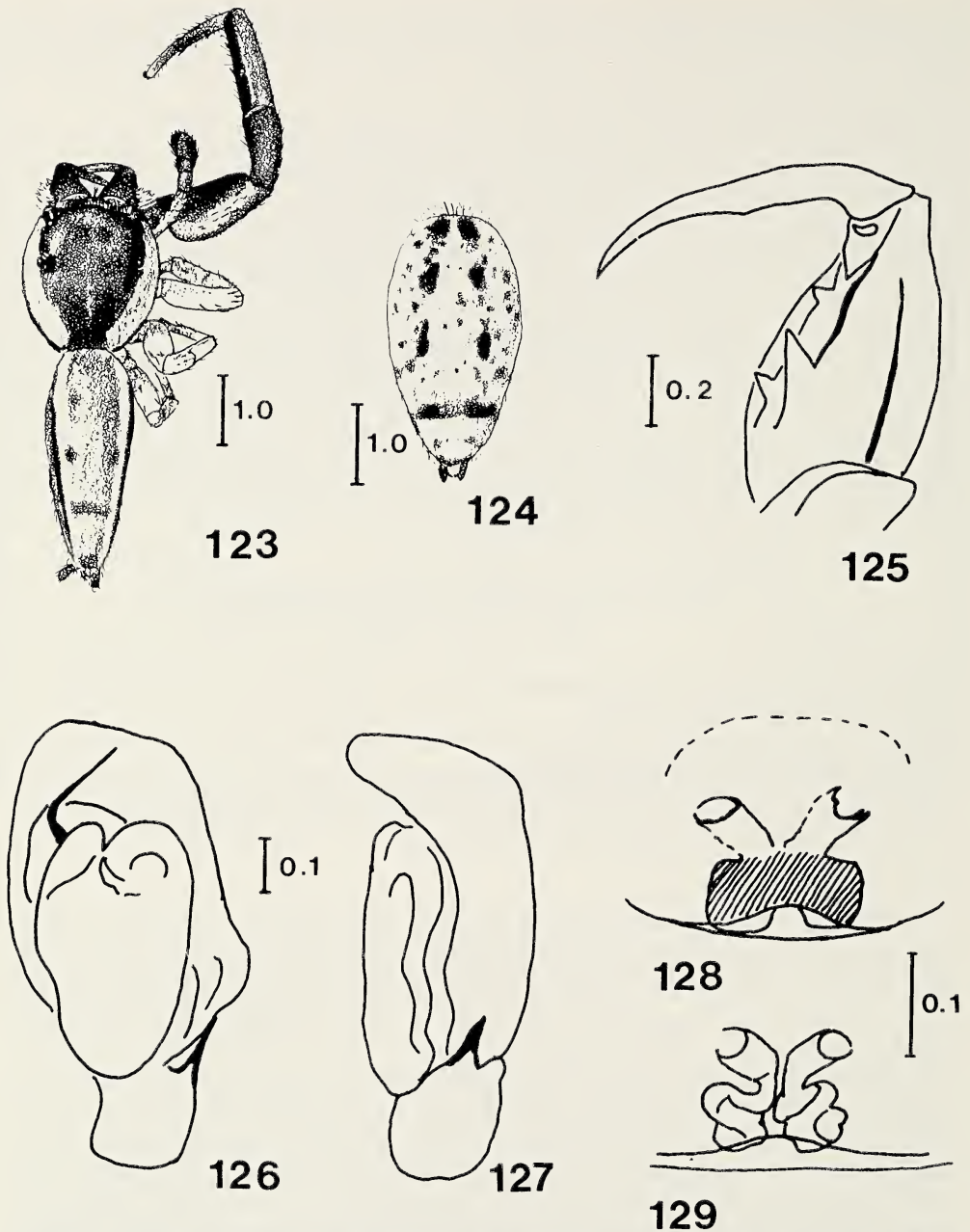
Parahentzia insignita Chickering 1946:316 (holotype male and allotype female from Panama Canal Zone in MCZ examined). NEW SYNONYMY.

Maeviobeata charitonovi Caporiacco 1947:34; 1948:734 (holotype male and paratype male and female from Guyana in the Museo Zoologico "La Specola," Florence, Italy, examined by M. E. Galiano - synonymy based on her drawings). NEW SYNONYMY.

H. parallela Roewer 1954:1218.

Diagnosis.—Males differ from all other *Hentzia* except *H. vittata* in having massive chelicerae with a slanted, spike-like retromarginal tooth (Fig. 125). They differ from *H. calypso* in size dorsal pattern and distribution. Female epigynum (Figs. 128, 129) diagnostic, with trumpet-like openings and rectangular spermathecal area.

Male.—Total length 3.95-5.15. Carapace 1.60-2.07 long, 1.35-1.85 wide, 0.70-1.06 high at PLE. Ocular area 0.70-0.90 long, 1.05-1.42 wide anteriorly, 1.15-1.53 wide posteriorly. Chelicerae 0.50-1.00 long, 0.35-0.60 wide (10 males from Boquete, Panama and 8 from Canal Zone, Aruba, Curaçao and Trinidad. Total 18). PME closer to ALE than to PLE. Leg formula 1423. Carapace red-brown; band of white hairs laterally, often followed by a wide black band to margin. Black around eyes, except brown around AME. Clypeus red-brown covered with white hairs. Chelicerae red-brown. Endites and labium, red-brown, often with lighter distal tips. Sternum red-brown. Abdomen orange to red-brown, often without markings or with four dark spots dorsally followed by two bands just anterior to spinnerets. There is occasionally a lighter longitudinal band on each side of the dorsum. Darker lateral areas. Venter gray to brown, in at least one case with three rows of small light dots. First legs red-brown, darker on prolateral surface of femora, patellae and tibiae. Other legs yellow. Pedipalpi yellow to red-brown, cymbium slightly darker.



Figures 123-129.—*Hentzia parallela* (Peckham and Peckham): 123, 124, from Fort Randolph, Canal Zone, Panama; 123, male, dorsal view; 124, female, dorsal view of abdomen; 125, left chelicera of male (holotype of *Parahentzia insignita* Chickering) from Canal Zone, Panama, ventral view; 126, 127, palp of male from Oranjstad, Aruba; 126, ventral view; 127, retrolateral view; 128, 129, epigynum of female from Panama; 128, ventral view; 129, dorsal view.

Female.—Total length 3.75-5.70. Carapace 1.70-1.95 long, 1.30-1.60 wide, 0.65-0.77 high at PLE. Ocular area 0.65-0.85 long, 1.05-1.30 wide anteriorly and 1.15-1.39 wide posteriorly. Chelicerae 0.35-0.50 long, 0.30-0.41 wide (12 females from Panama and Canal Zone). PME closer to ALE than to PLE. Leg formula 1423.

Carapace orange with darker paired dorsal posterior and lateral longitudinal bands. Black around eyes, except brown around AME. Clypeus orange. Chelicerae orange. Endites and labium orange, lighter on distal tips. Sternum orange. Abdomen yellow with two longitudinal rows of four brown spots each, followed by a thin band of thick dark brown spots just anterior to the spinnerets. All legs yellow-orange. Pedipalpi yellow, unmarked.

Distribution.—Trinidad, Guyana, Aruba, Curaçao, Costa Rica, Honduras and Panama (Map 7).

Natural history.—Males have been collected in January, June-August and November-December. Females from June-August and November. They are probably found as adults all year.

Specimens examined.—ARUBA: Oranjested (AMNH). COSTA RICA: Monteverde (AMNH). CURAÇAO: Piscadera Bay (AMNH). HONDURAS: Lancetilla (MCZ). PANAMA: Boquete (MCZ), Canal Zone (Barro Colorado) (MCZ), El Valle (AMNH). TRINIDAD: East Coast (MCZ), Piarcó (AMNH).

Hentzia calypso, new species

Figs. 130-136, Map 5

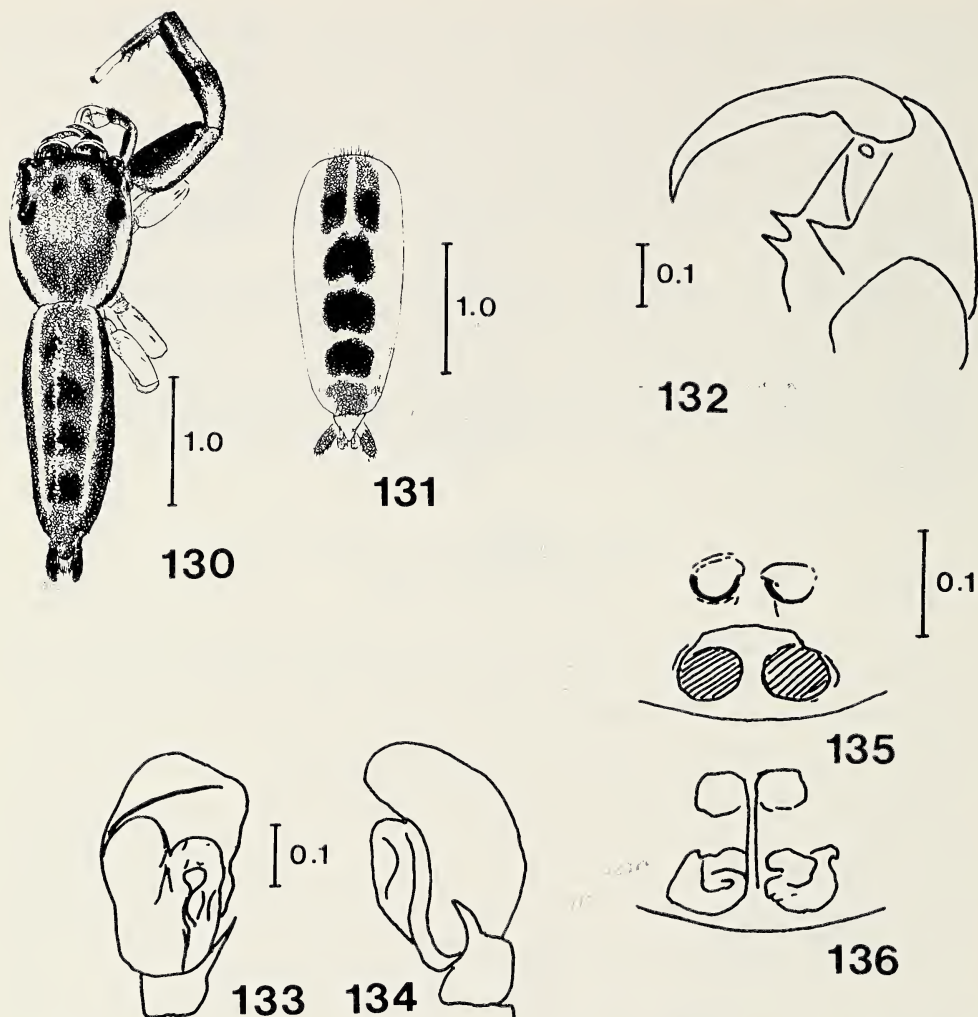
Types.—Male holotype from 2 mi. SW Unity Valley, Jamaica (18 March 1955; A. M. Nadler), deposited in the AMNH. Male and female paratypes from Jamaica deposited in the AMNH and the MCZ.

Etymology.—The specific name refers to the sea nymph in Homer's *Odyssey* and also a style of music found in the southern Caribbean.

Diagnosis.—*Hentzia calypso* is one of the smallest species of the genus, males being less than 4.0 mm and females from 3.5 to 4.5 mm in length. The structure of the male chelicerae is similar to that of *H. vittata*, but the body is much more elongate and the dorsal pattern is distinctive (Figs. 130, 131). Female epigynum diagnostic, with large openings and oval spermathecae internally (Figs. 135, 136); externally similar to those of *H. chekika* and *H. poenitens* (Fig. 135). It differs from the former species in size, internal structure of epigynal tubes, pattern and distribution and from the latter in internal structure of epigynum, pattern and distribution.

Male.—Total length 3.15-3.90. Carapace 1.25-1.50 long, 0.92-1.12 wide, 0.50-0.60 high at PLE. Ocular area 0.55-0.70 long, 0.80-0.95 wide anteriorly and 0.82-0.95 wide posteriorly. Chelicerae 0.25-0.50 long, 0.23-0.32 wide (four males from Jamaica). PME slightly closer to PLE than to ALE. Leg formula 1423. Carapace red-brown with white lateral bands. Black around eyes except AME, which is dark brown. Clypeus red-brown. Chelicerae dark brown. Endites dark brown with prolateral 1/3 lighter. Labium dark brown with lighter anterior 1/3. Sternum red-brown. Abdomen dark red-brown with darker squarish spots and white lateral stripes dorsally (Fig. 130). Venter gray-brown. First legs yellow-brown with darker brown on prolateral and ventral femora, patellae and tibiae. Darker bands on distal patellae, distal and proximal tibiae and distal metatarsus. Tarsus yellow. Other legs yellow. Pedipalpi with yellow cymbium, dark brown patellae and tibiae, and femur with yellow dorsally, dark brown prolaterally.

Female.—Total length 3.50-4.45. Carapace 1.50-1.65 long, 1.10-1.30 wide, 0.55-0.70 high at PLE. Ocular area 0.60-0.70 long, 0.95-1.00 wide anteriorly and 0.95-1.10 posteriorly. Chelicerae 0.25-0.40 long, 0.25-0.30 wide. PME closer to PLE



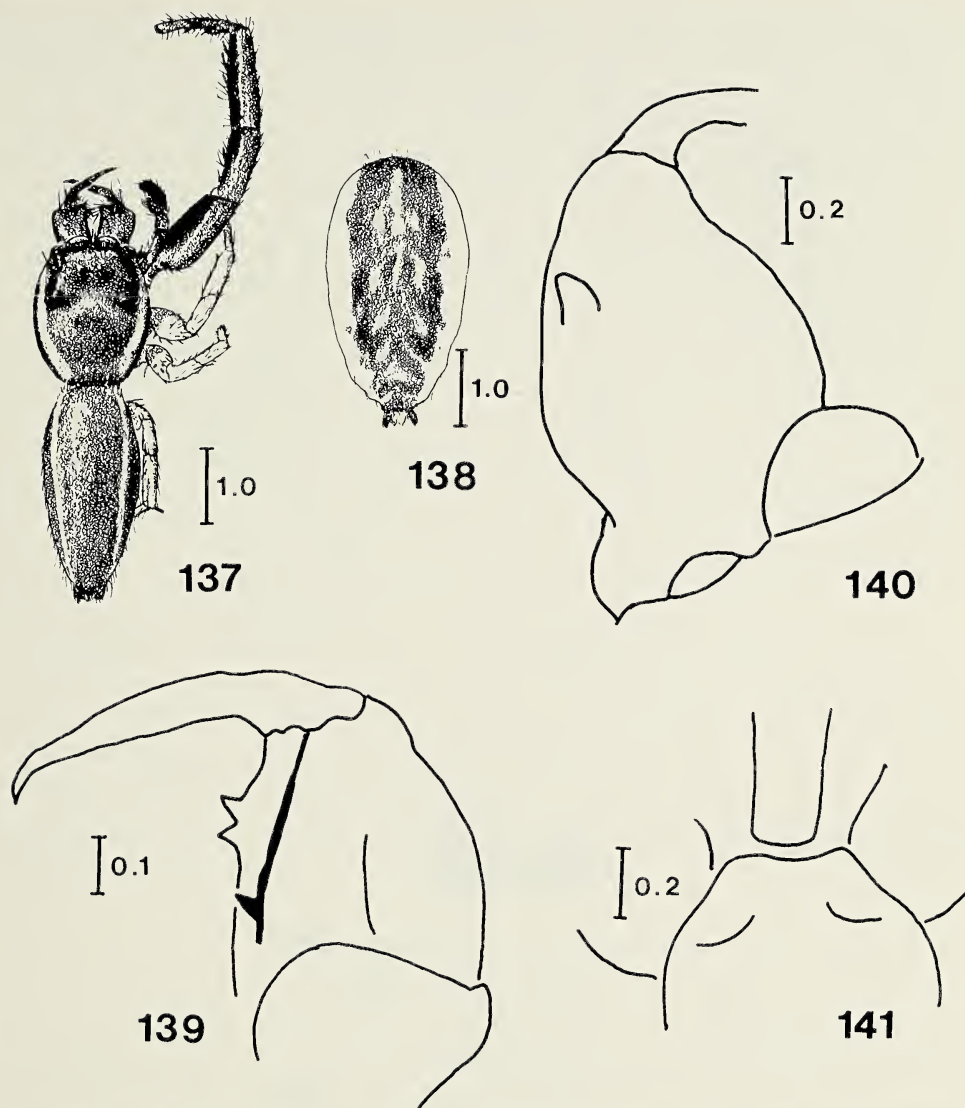
Figures 130-136.—*Hentzia calypso* n. sp.: 130-134, from Unity Valley, Jamaica; 130, male, dorsal view; 131, female, dorsal view of abdomen; 132, left chelicera of male, ventral view; 133, 134, palp of male; 133, ventral view; 134, retrolateral view; 135, 136, epigynum of female from Roundhill, Jamaica; 135, ventral view; 136, dorsal view.

than to ALE. Leg formula 1423. Carapace orange, black around eyes except AME; brown around AME; darker lateral to midline, lighter along margin. Clypeus covered with white hairs. Chelicerae, endites and labium orange. Sternum yellow. Abdomen yellow with dark brown markings as in male. Streaks laterally forming rough stripes. Venter yellow. First legs yellow with dark stripe on prolateral femora and prolateral distal tibiae. Spots on retrolateral distal and proximal tibiae, distal femora and patellae. Other legs and pedipalpi yellow.

Distribution.—Known only from Jamaica (Map 5).

Natural history.—Males from March and November. Females from July and November. Probably adults can be collected all year.

Specimens examined.—JAMAICA: Buff Bay (MCZ), Manderville (FSCA), New Castle (MCZ), Roundhill (AMNH), St. Andrew (MCZ), St. Catherine (AMNH).



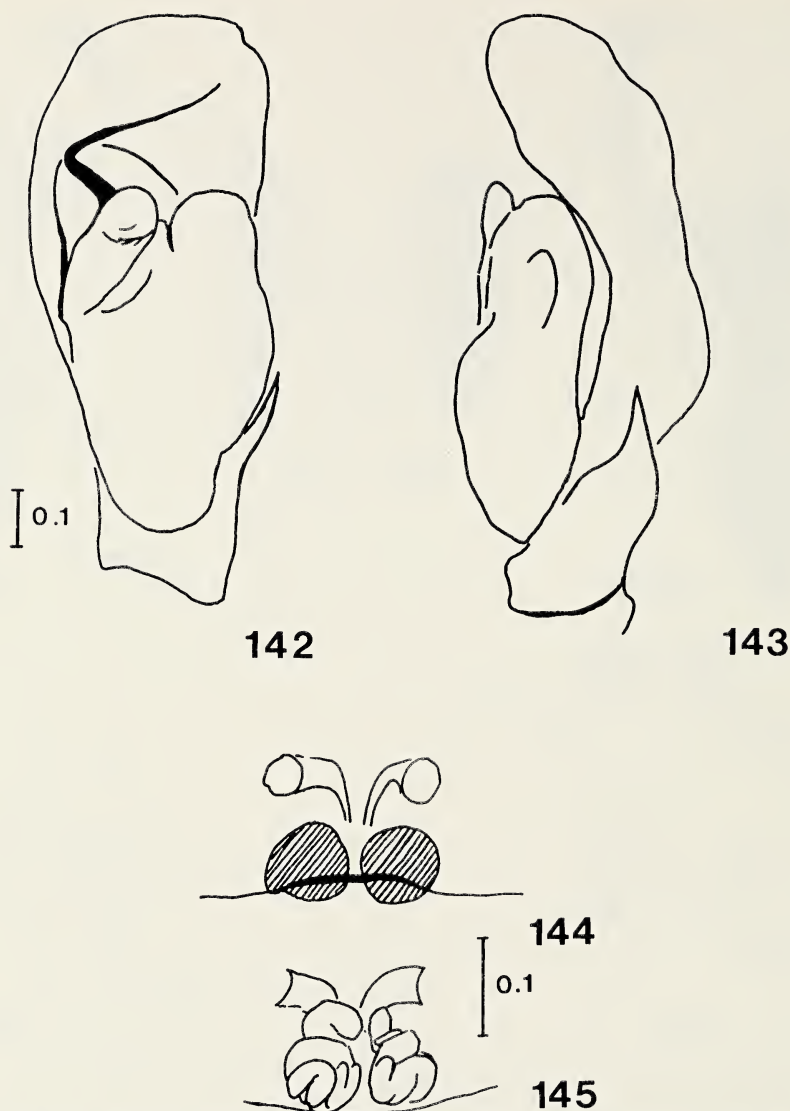
Figures 137-141.—*Hentzia mandibularis* (Bryant): 137, 138, from Dept. L'Oeste, Haiti; 137, male from Morne d'Enfer, dorsal view; 138, female from Parc National de la Viciite, dorsal view of abdomen; 139, left chelicera of male from Port-au-Prince, Haiti, ventral view; 140, 141, holotype male from the Dominican Republic; 140, left chelicera, dorsal view, showing tubercle; 141, anterior sternum, ventral view showing depressions.

Hentzia mandibularis (Bryant)

Figs. 137-145, Map 4

Parahentzia mandibularis Bryant 1943:500 (holotype male from foothills of Cordillera Central S of Santiago, Dominican Republic, in MCZ examined).

Diagnosis.—Although *H. mandibularis* is atypical in that males may have a pronounced tubercle on the dorsal chelicerae, it is certainly a *Hentzia* and is related to *H. vittata*. They may also have the depressions in the sternum mentioned by Bryant, or they may lack them. The males differ from other



Figures 142-145.—*Hentzia mandibularis* (Bryant): 142, 143, palp of holotype male; 142, ventral view; 143, retrolateral view; 144, 145, epigynum of female from La Decouverte, Haiti; 144, ventral view; 145, dorsal view.

Hentzia males with thick and short chelicerae by the position and size of the retromarginal tooth (Fig. 139) the presence in some males of a dorsolateral tubercle on the chelicerae (Fig. 140), the narrow labium and the presence in some males of two depressions in the anterior sternum (Fig. 141). The structure of the epigynum, with circular openings, is diagnostic for females (Figs. 144, 145).

Male.—Total length 3.70-5.17. Carapace 1.55-2.13 long, 1.20-2.05 wide, 0.70-1.15 high at PLE. Ocular area 0.75-0.90 long, 1.00-1.31 wide anteriorly and 1.18-1.48 wide posteriorly. Chelicerae 0.50-1.15 long, 0.30-0.57 wide (seven males from Haiti and the Dominican Republic). PME closer to ALE than to PLE. Leg formula 1423. Carapace red-brown with white bands laterally. Eyes surrounded by black, except AME, surrounded by dark brown. Clypeus covered with white

hairs. Chelicerae red to orange-brown. Endites, labium and sternum red to orange-brown with two indentations on anterior sternum (Fig. 141). Abdomen red to orange-brown with white dorsolateral bands. Lateral area gray-brown; venter red to gray-brown. Scattered iridescent scales and often with darker markings in central dorsal portion. First legs red-brown, darker anteriorly and ventrally. Tarsus lighter. Other legs whitish to orange. Pedipalpi red-brown, bulb and cymbium darker.

Female.—Total length 4.15-4.84. Carapace 1.71-1.80 long, 1.35-1.40 wide, 0.70-0.77 high at PLE. Ocular area 0.77-0.80 long, 1.06-1.10 wide anteriorly and 1.20-1.25 wide posteriorly. Chelicerae 0.50-0.90 long 0.30-0.35 wide (three females from Haiti). PME closer to ALE than to PLE. Leg formula 1423. Carapace red-brown with scattered black hairs, white scales laterally and iridescent scales dorsally, especially between eyes. Clypeus covered with white hairs. Chelicerae orange-brown, without tubercles. Endites dark brown with pale tips. Labium dark brown. Sternum red-brown. Abdomen red-brown with white streaks and spots and lateral bands. Lateral area red-brown, venter whitish. First legs yellow-brown, darker ventrolaterally on femur and on distal tibia, patella and metatarsus. Metatarsus-tarsus generally yellow. Other legs white. Pedipalpi yellow; proximal brown spots on dorsal tibia, patella and tarsus.

Distribution.—Known only from the island of Hispaniola (Map 4).

Variation.—Specimens may have or lack distinct depressions in the sternum. Males may have dorsal chelicerai tubercles or may lack them, or have only traces.

Natural history.—Males have been collected in March and May-July. Females are known only from March and May.

Specimens examined.—DOMINICAN REPUBLIC: Foothills Cordillera Central S of Santiago (MCZ). HAITI: Dept. L'Oeste,; Parc National de la Vicite (FSCA), Morne d'Enfer (FSCA), Kenscoff (AMNH), Port-au-Prince (MCZ).

Hentzia squamata (Petrunkévitch)

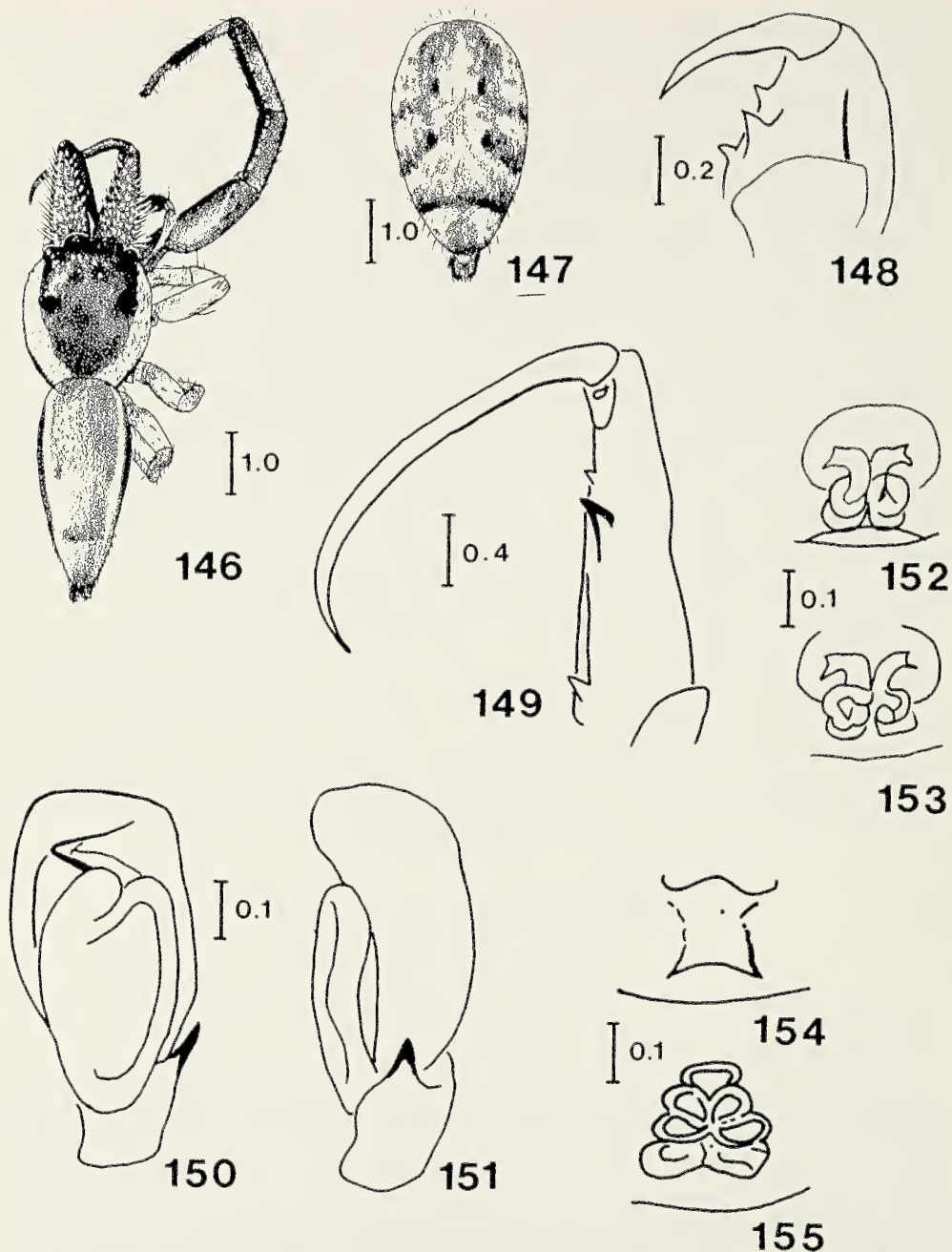
Figs. 146-153, Map 5

Wala squamata Petrunkevitch 1930:146 (holotype and paratypes from Mona Island in AMNH examined).

Hentzia squamata Bryant 1947:93.

Diagnosis.—Males differ from all other *Hentzia* in having white scales nearly covering chelicerae (Fig. 146). Females resemble females of *H. antillana* closely and can be easily separated only by association with males. Males also differ from males of *H. antillana* in the arrangement and structure of the chelicerai teeth (Figs. 148, 149), which place it in the *vittata* species group.

Male.—Total length 3.69-5.44. Carapace 1.77-2.48 long, 1.48-2.12 wide, 0.89-1.18 high at PLE. Ocular area 0.83-1.06 long, 1.21-1.53 wide anteriorly and 1.30-1.59 wide posteriorly. Chelicerae 0.59-2.12 long, 0.44-0.65 wide (eight males from Mona Island). PME closer to ALE than to PLE. Leg formula 1423. Carapace red-brown, yellowish in ocular area and with lateral white scales. Eyes ringed with black. Clypeus covered with white hairs. Chelicerae yellow-brown, covered with pearly scales. Endites and labium yellow-brown with light distal tips. Sternum yellow-brown. Abdomen yellow-brown with darker markings (Fig. 146) and with light dorsolateral stripes, followed by dark lateral stripes. Venter yellow-



Figures 146-153—*Hentzia squamata* (Petrunkévitch) from Mona Island: 146, male, dorsal view; 147, female, dorsal view of abdomen; 148, left chelicera of male, ventral view; 149, left chelicera of another male, ventral view; 150, 151, palp of holotype male; 150, ventral view; 151, retrolateral view; 152, 153, epigynum of female; 152, ventral view; 153, dorsal view.

Figures 154-155.—*Hentzia zombia* n. sp., epigynum of female from Roche Platte, Haiti; 154, ventral view; 155, dorsal view.

brown. First legs yellow-brown. Other legs lighter yellow-brown. Pedipalpi yellow brown with dark dorsal spot on tibiae.

Female.—Total length 4.13-6.67. Carapace 1.89-2.48 long, 1.59-2.18 wide, 0.83-1.06 high at PLE. Ocular area 0.83-1.06 long, 1.24-1.53 wide anteriorly and 1.36-1.77 wide posteriorly. Chelicerae 0.53-0.89 long, 0.35-0.59 wide (11 females from Mona Island). PME closer to ALE than to PLE. Leg formula 1423. Carapace red-brown, yellow in ocular area. Eyes ringed in black except AME ringed in brown. Clypeus covered with white hairs. Chelicerae red or yellow-brown. Endites and labium red-brown with lighter distal tips. Sternum yellow-brown. Abdomen yellow with brown markings much like *H. antillana* (Fig. 147). Venter yellow. First legs yellow-brown. Other legs lighter yellow-brown. Pedipalpi yellow with dorsal proximal spots except on femora.

Distribution.—Known only from Mona Island (Map 5).

Natural history.—Males collected in February, April and August. Females in August. Probably found all year, but the island is little collected because of difficulties of access.

Specimens examined.—PUERTO RICO: Mona Island (AMNH, MCZ).

Hentzia zombia, new species

Fig. 154, 155, Map 6

Types.—Female holotype from Morne d'Enfer, Dept. L'Oeste, Haiti (5 May 1984, M. C. Thomas) deposited in the FSCA.

Etmology.—The specific name refers to the "living dead" of West Indian voodoo.

Diagnosis.—While females have the major characteristics of the genus—hair pencils, spatulate hairs on femora and external genitalia similar to several described species, such as *H. fimbriata* (Fig. 154), it is easily distinguished from all other species by its large size (about 7 mm), stocky build and covering of pink iridescent scales. The internal epigynal structure (Fig. 155) is unlike any other *Hentzia*. It is at present difficult to place this species in a species group, but it is assumed to be related to *H. vittata* because of its general body shape and the structure of the external epigynum.

Female.—Total length 6.60-7.10. Carapace 2.60-2.90 long, 2.20-2.45 wide, 1.20 high at PLE. Ocular region 1.15-1.20 long, 1.45-1.60 wide anteriorly and 1.60-1.80 wide posteriorly. Chelicerae 0.90-1.00 long, 0.70-0.80 wide (two females from Haiti). PME closer to ALE than to PLE. Leg formula 1423. Carapace dark brown. Eye region dark with black around all eyes except dark brown around AME. Clypeus dark brown. Chelicerae dark red-brown. Endites and labium dark brown with white tips. Sternum orange. Coxae orange. Abdomen dark brown to yellow, with darker markings consisting of four dark patches on the posterior dorsal two-thirds and two dark streaks just anterior to spinnerets which nearly join at midline. Venter brown. First legs brown; lateral femora darker; tarsus yellow. Other legs yellow. Pedipalpi dark brown; tarsi lighter on distal 2/3. Body covered with iridescent pink scales.

Distribution.—Known only from Haiti (Map 6).

Natural history.—Collected in February and May.

Specimens examined.—HAITI: Morne d'Enfer (FSCA), Roche Platte (FSCA).

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Hentschel, E. and W. B. Muchmore. 1989. *Cocinachernes foliosus*, a new genus and species of pseudoscorpion (Chernetidae) from Mexico. J. Arachnol., 17:345-349.

**COCINACHERNES FOLIOSUS, A NEW GENUS AND SPECIES
OF PSEUDOSCORPION (CHERNETIDAE)
FROM MEXICO**

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ABSTRACT

The new genus and species *Cocinachernes foliosus* is described, based on specimens from Isla Cocinas, Estado de Jalisco, México. It is unique in the form of the spermathecae of the female.

INTRODUCTION

In recent years increasing attention has been paid to the spermathecae of females in the taxonomy of pseudoscorpions in the family Chernetidae (see Muchmore 1975; Muchmore and Hentschel 1982; Mahnert 1979, 1985). A number of species with similar external features have proved to possess quite different female genitalia (spermathecae), for example, *Epactiochernes* compared to *Dinocheirus* (Muchmore 1974), and *Americhernes* compared to *Lamprochernes* (Muchmore 1976). Here we present the description of a genus which is quite similar externally to *Illinichernes* Hoff or *Ceriochernes* Beier but which has a unique form of spermatheca.

***Cocinachernes*, new genus**

Type species.—*Cocinachernes foliosus*, new species.

Diagnosis.—A genus of the family Chernetidae Chamberlin. Carapace and pedipalps moderately sclerotized, deep reddish-brown in color. Surface of carapace, palps and abdominal sclerites reticulate, with stout, wide, pinnately feathered and leaflike vestitural setae. Carapace with 2 transverse furrows, without eyes or ocular spots, and with about 60 pinnately feathered setae more or

less arranged in 8 transverse rows. Tergites 1-10 divided; sternites 4-10 divided; pleural membranes longitudinally rugose and slightly papillose. Tergites with 6 to 12 pinnately feathered, palmate setae arranged in a single row; sternites with 8 to 12 smaller marginal setae, slightly denticulate on anterior ones, changing gradually to pinnately feathered shape on posterior ones. Setae on stigmal and anal plates short and acuminate. Cheliceral hand with 7 setae, *b* and *sb* terminally denticulate, *es* short and acuminate, both accessory setae acuminate (proximal one possibly denticulate); flagellum of 4 setae, the 2 basal ones short and lying close together, the distal one unilaterally serrate along distal margin; galea of female moderate in size, with 6 small branches, that of male smaller and without branches. Palps robust, slightly larger in female; surface of palps reticulate except for fingers, with pinnately feathered setae on all segments except movable finger. Two especially long, slightly feathered setae on inner surface of chelal hand near base of fixed finger, and 3 similar long setae arranged in a row on dorsal side of fixed finger. Trichobothrium *st* on movable finger closer to *t* than to *sb* and near middle of finger; *ist* on fixed finger distinctly distad of *est*, which is near middle of finger. Venom apparatus well developed in movable chelal finger, vestigial or absent in fixed finger; each finger with 29-32 marginal teeth and with several external and 1 or no internal accessory teeth. Legs rather slender, with pinnately feathered, denticulate, and acuminate setae. Tarsus of leg IV without any tactile seta. Anterior genital operculum of male with a group about 35 setae, including 4 larger ones medially; posterior operculum with 20 setae on face and along posterior margin. Female anterior genital operculum with 23-24 short setae on face; posterior operculum with a row of 15-16 setae on face and along posterior margin; spermatheca in form of four short, broad tubes attached to a spherical base.

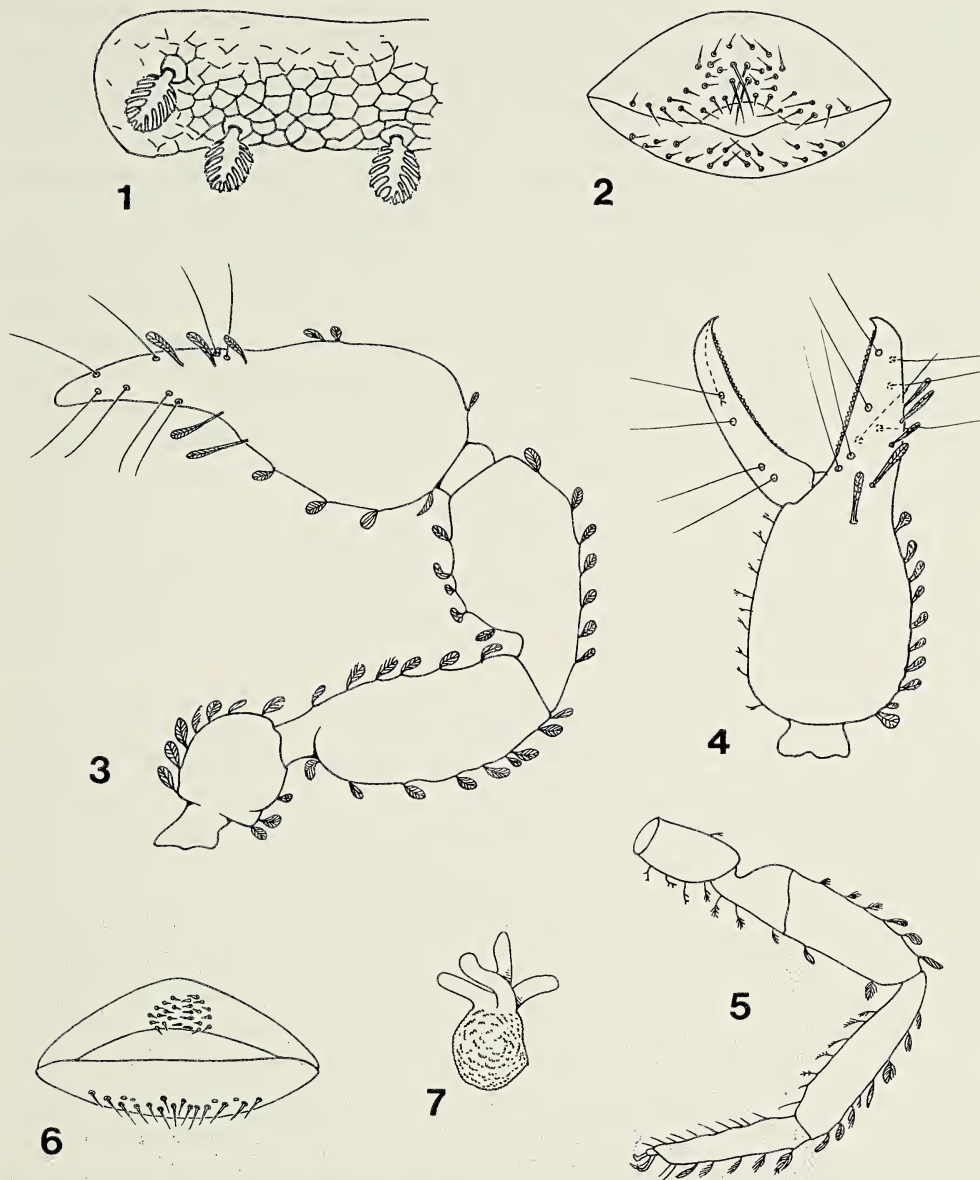
Etymology.—The genus is named after the island Cocinas, where it was collected.

Remarks.—This new genus shares a number of important characters with *Illinichernes* Hoff (1949) from the United States: four setae in cheliceral flagellum, absence of a tactile seta from tarsus IV, presence of accessory setae on the cheliceral hand, the peculiar leaflike setae on body and appendages, and the long clavate setae on the fixed chelal finger. But it differs radically from *Illinichernes* in the form of the spermathecae: four short tubules extending from a central globose chamber in *Cocinachernes*, two long thin tubules with expanded ends in *Illinichernes* (see Benedict and Malcolm 1982: fig. 5). Also *Cocinachernes* is quite similar in respect to its integument and leaflike setae to *Ceriochernes foliaceosetosus* Beier (1974) from Brasil, but differs in having four rather than three setae in the flagellum. It differs from *Ceriochernes*(?) *amazonicus* Mahnert (1985) in the nature of both the vestitural setae and the spermathecae.

Cocinachernes foliosus, new species

Figs. 1-7

Types.—México, Estado de Jalisco, Islas Cocinas, in dry litter 200 m from shore, 9 September 1981 (J. G. Palacios): male holotype and 2 female paratypes, deposited in the Arachnid Collection of the Laboratorio de Acarología, Facultad de Ciencias, Universidad Nacional Autónoma de México, México DF.



Figures. 1-7.—*Cocinachernes foliosus*, new species: 1-5, male; 1, part of tergite, showing reticulated surface and leaflike setae; 2, genital opercula; 3, right palp, dorsal view; 4, left chela, lateral view; 5, leg IV; 6, 7, female; 6, genital opercula; 7, spermathecae.

Description of male (based on holotype).—Surface of carapace, tergites, posterior sternites palps (except fingers), and legs lightly to moderately sclerotized and moderately to heavily reticulate, each space with more or less hexagonal shape, except for the small area surrounding the insertion of each seta, which is smooth (Fig. 1). Vestitural setae on these parts of the body broad, pinnately feathered, leaflike, with a middle axis and 9 to 12 lateral ribs, which are often arranged opposite one another, the pair of basal ribs always much shorter and thinner than the rest; each seta standing on a small tubercle (Fig. 1). Carapace subtriangular, as long as posterior breadth, with two distinct transverse furrows,

without eyes or ocular spots; surface heavily reticulate, with 62 vestitural setae more or less arranged in 8 transverse rows, 7 setae near anterior margin and 6 near posterior margin, setae along lateral margins smaller than those on face of carapace. Tergites 1-10 and sternites 4-10 divided; surfaces of tergites heavily reticulate; anterior sternites almost smooth, changing gradually to a heavily reticulate surface on the posterior ones; pleural membranes longitudinally rugose and slightly papillose; all dorsal setae well developed in a pinnately feathered shape, except for the acuminate ones on the anal plate; setae of sternites acuminate on the genital, stigmal and anal plates, denticulate on anterior sternites, and changing gradually to a pinnately feathered shape on posterior sternites, but always smaller than setae on the dorsum of body. Tergal chaetotaxy of holotype 6:8:6:8:8:9:9:11:10:11:10:2; and sternal chaetotaxy 37:(3)20(3):(1)8(1):17:13:12:10:10:8:6:2. 37 setae on face of anterior genital operculum, of which the 4 in the middle are longer; posterior operculum with 20 setae, arranged more or less in 2 rows on face and posterior margin (Fig. 2). Internal genitalia of usual chernetid type, well sclerotized and distinct.

Chelicera $1/3$ as long as carapace; hand with 7 setae, *b* and *sb* terminally denticulate, *es* short and acuminate, distal accessory seta acuminate proximal one slightly denticulate; flagellum of 4 setae, the 2 basal ones short and lying close together, and the distal one heavily dentate along distal margin; galea short and simple, without denticles.

Palp stout (Fig. 3), with chelal hand a little broader than deep; femur 2.75, tibia 1.8, and chela (without pedicel) 2.5 times as long as broad; hand (without pedicel) 1.4 times as long as deep; movable finger 0.97 as long as hand. Surface of palp moderately reticulate except for fingers; setae pinnately feathered except for those on ventral margin of hand, which are less developed or denticulate and those on fingers, which are acuminate; 5 especially long, pinnately feathered setae on fixed finger, a row of 3 on dorsal side near middle and 2 on internal face near base of finger. Trichobothria as indicated in Fig. 4. Fixed finger with 30 contiguous, cusped marginal teeth, and 5 external plus 1 internal accessory teeth; movable finger with 31 similar marginal teeth and 5 external (no internal) accessory teeth; venom apparatus well developed only in movable finger.

Legs slender, with moderately reticulate surfaces and with pinnately feathered setae except on internal margins, where setae are smaller and denticulate or acuminate; leg IV (Fig. 5) with entire femur 3.95 times as long as deep; tarsus lacking a tactile seta.

Description of female (based on the 2 paratypes).—Much like male, but slightly more robust; genital opercula as shown in Fig. 6; anterior operculum with a compact Ω -shaped group of 23-24 short setae on face, posterior operculum with 15-16 setae on face and along posterior margin; spermathecae in form of four short, broad tubes extending from a globose chamber with a rugose surface (Fig. 7). Cheliceral galea better developed than in male, with 6 small rami. Palp much as in male, but slightly larger; femur 2.8, tibia 2.05-2.1, and chela (without pedicel) 2.45-2.55 times as long as broad; hand (without pedicel) 1.3-1.4 times as long as deep; movable finger 0.94-1.03 times as long as hand. Fixed finger with 29-31 marginal teeth, and 5-7 external and 1 or no internal accessory teeth; movable finger with 32 marginal teeth, 3-4 external and no internal accessory teeth.

Measurements (mm).—Figures given first for holotype male, followed in parentheses by those for the paratype females. Body length 2.13 (2.41-2.55). Carapace length 0.68 (0.74-0.78). Chelicera length 0.225. Palpal femur 0.59 (0.67) by 0.215 (0.24); tibia 0.525 (0.58-0.59) by 0.29 (0.28); chela (without pedicel) 0.83 (0.93-0.94) by 0.335 (0.37-0.38); hand (without pedicel) 0.44 (0.48-0.495) by 0.315 (0.36-0.37); pedicel length about 0.10; movable finger length 0.425 (0.47-0.495). Leg IV: entire femur 0.495 (0.54-0.57) by 0.125 (0.12-0.14); tibia 0.41 (0.44-0.45) by 0.08 (0.095-0.10); tarsus 0.335 (0.355-0.37) by 0.07 (0.08).

Etymology.—The species is named *foliosus* for the leaflike appearance of the vestitural setae.

Remarks.—In this species the female is larger than the male, but the proportions of the palps are about the same in the two sexes. It is interesting to note the considerable reduction in the number of setae, a condition apparently related to the increase in breadth of the setae.

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**FURTHER REVISION OF SOME NORTH AMERICAN
FALSE SCORPIONS ORIGINALLY ASSIGNED TO
MICROCREAGRIS BALZAN
(PSEUDOSCORPIONES, NEOBISIIDAE)**

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ABSTRACT

The type specimens of six North American species, originally described in the genus *Microcreagris* Balzan have been re-examined. Of these, five species belong to four *Microcreagris*-related genera. These are: *T. lata* (Hoff) in *Tuberocreagris* Čurčić, *C. laudabilis* (Hoff) in *Cryptocreagris* Čurčić, *A. mortis* (Muchmore) in *Alabamocreagris* Čurčić, and *A. reddelli* (Muchmore) and *A. texana* (Muchmore) in *Australinocreagris* Čurčić. A new genus, *Minicreagris*, has been proposed, with *Microcreagris pumila* (Muchmore) as its type species. Genital areas and trichobothrial patterns are figured, and brief diagnoses and some taxonomic and distributional data for the genera and species examined are given. A key to the *Microcreagris*-related genera of North America north of Mexico is presented.

Considerable confusion has surrounded the identity of members of the genus *Microcreagris* Balzan, 1892. This was in part due to the difficulty in obtaining type specimens, but to a greater extent to inadequate original description of the type species, *M. gigas* Balzan, 1892, from Asia. In addition, the long used character of galeal form has shown to be of limited value. It was recently that the holotype of *M. gigas* was adequately redescribed by Mahnert (1979), and Čurčić (1983) did the same for the other known species, *M. herculea* Beier, 1959. As currently defined, the genus *Microcreagris* is restricted to China and Afghanistan (Čurčić 1983, 1985, 1986).

Some of the available pseudoscorpions, previously assigned to the genus *Microcreagris* and present in North America north of Mexico (Beier 1931, 1932; Hoff 1945, 1958; Chamberlin 1952, 1962; Muchmore 1966, 1969), have been revised by Čurčić (1978, 1981, 1982a, 1984). The type material of some United States species, along with some undetermined U.S. species, has been re-examined. From this study, ten new genera have been proposed and described (Čurčić 1984). Thus the outstanding heterogeneity of "*Microcreagris*" in that area has been demonstrated.

In the present study, I have re-examined the type specimens (holotypes and allotypes) of six additional pseudoscorpion species of the "*Microcreagris*"-complex, which are deposited in the collection of the American Museum of Natural History in New York (AMNH). Of these, five species belong in four *Microcreagris*-related genera already reported from this region and one belongs to a new genus, *Minicreagris*.

The purpose of this paper is to further demonstrate the heterogeneity of "*Microcreagris*" in North America and to present objective criteria for the identification of some North American genera of this complex. This study should also stimulate an analysis of the taxonomic rank of all other North American pseudoscorpions currently assigned to "*Microcreagris*."

Family NEOBISIIDAE Chamberlin, 1930

Genus *Tuberocreagris* Čurčić, 1978

Diagnosis.—Galea with subterminal spinule(s). Abdominal sternites with one row of setae. Male genital area: sternite II with a group of median and posterior setae, sternite III with a transverse row of anterior setae, some intermediary setae, and a row of posterior marginal setae. Female genital area: sternite II with a group of setae on either side of the midline, sternite III with a transverse row of posterior setae.

Manducatory process with 3 setae. Femur and chelal palm of pedipalp with distinct granulations. Interiorly, an accessory tubercle on femur and two such tubercles on tibia. Trichobothriotaxy *esb* distal to *eb*; *ib-ist-isb* in proximal part of finger; *est* closer to *it* than to *ist*; *sb* and *st* equidistant from *b* and *t*, respectively.

Leg IV: tibia, basitarsus and telotarsus with one tactile seta each.

Type species.—*Ideobisium rufulum* Banks.

Subordinate taxa.—*Tuberocreagris rufula* (Banks), *T. lata* (Hoff).

Distribution.—District of Columbia and North Carolina, USA.

Remarks.—A thorough study of some congeneric specimens from Washington, D.C., has showed that the interior tubercles on pedipalpal femora and tibiae may be of different sizes, and sometimes inconspicuous and even difficult to establish (particularly when these podomeres are studied on fixed slide preparations) (Čurčić, MS).

Tuberocreagris lata (Hoff), new combination

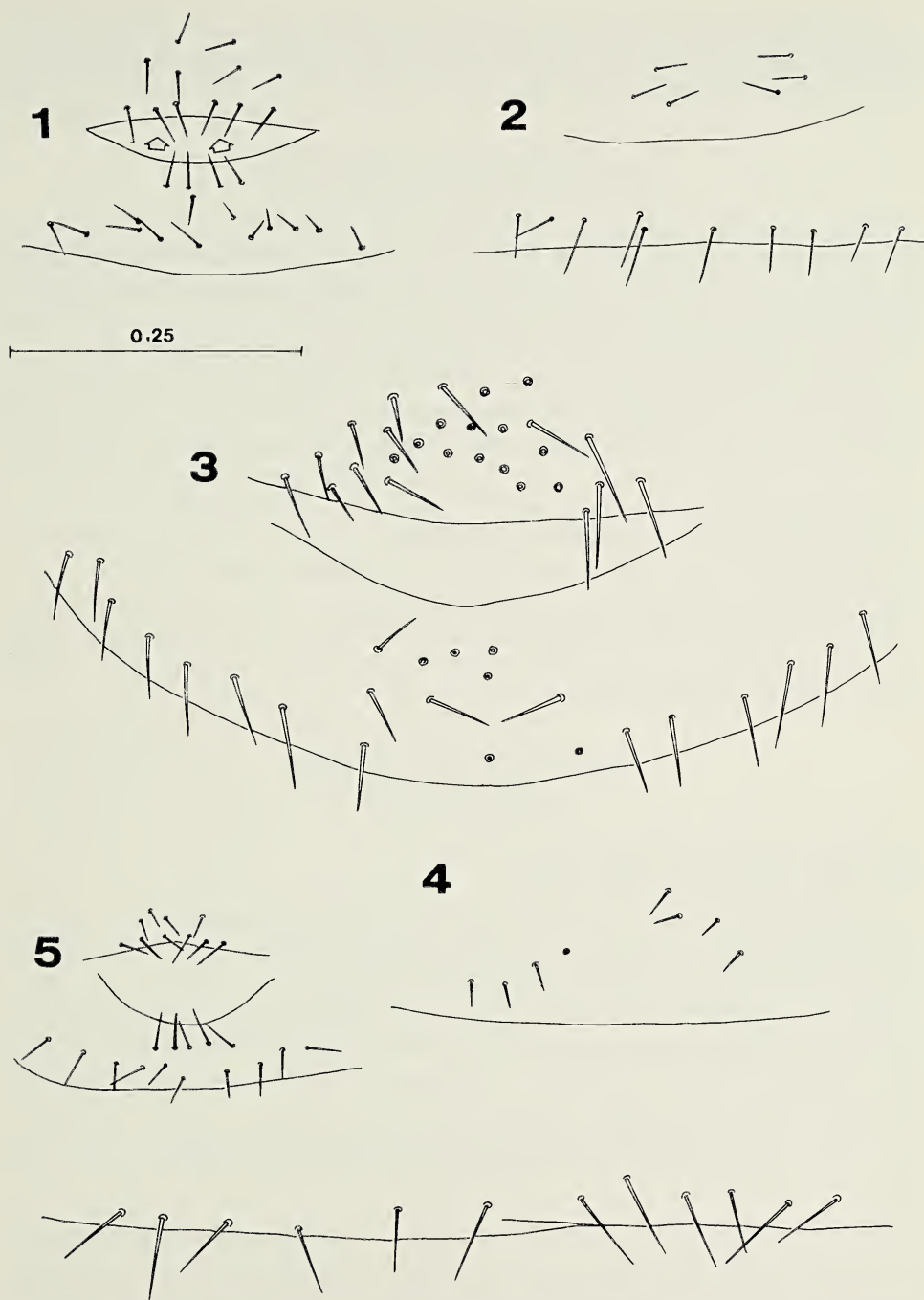
Figs. 1, 2, 9, 10

Microcreagris lata Hoff, 1945:323, 1958:12.

Diagnosis.—Epistome small and apically rounded. Carapace with $4 + 4 + 6 + 6 + 6 = 26$ (male) and $4 + 6 + 6 + 6 + 7 = 29$ setae (female). Two pairs of eyes resembling eye-spots. Galea with several terminal branchlets.

Tergites I-X with 6-9-11-11-11-12-11-13-12-11 (male), or 6-9-11-11-12-11-12-12-13-12 setae (female). *Male genital area:* sternite II with 12 setae (of these, six setae are found along the posterior sternal margin), sternite III with 4 anterior, 3 intermediary and 10 posterior setae, and 4 or 5 microsetae along each stigma. *Female genital area:* sternite II with 3 setae on each side of the midline, sternite III with 10 posterior setae and 5 or 6 suprastigmal microsetae on each side. Other sternites with one row of setae.

Pedipalps: fixed chelal finger with 51 or 52 (male) and 56 close-set, small and rounded and eventually square-topped teeth (female); some distal teeth are



Figures 1-5.—Genital area. 1, *Tuberoacreagris lata* (Hoff), holotype male; 2, *T. lata* (Hoff), allotype female; 3, *Cryptocreagris laudabilis* (Hoff), holotype male; 4, *C. laudabilis* (Hoff), allotype female; 5, *Minicreagris pumila* (Muchmore), holotype male. Scale in mm.

asymmetrically pointed. Movable chelal finger with 51 (male) or 60 small, close-set and rounded teeth (female); few distal teeth are asymmetrical.

Distribution.—North Carolina, USA.

Specimens examined.—Holotype male (C. Clayton Hoff 5610-S-419.1) and allotype female (C. Clayton Hoff 5611-S-419.2), from oak litter, sandy soil, Duke Forest, Durham, North Carolina, 16 September 1944 (A. S. Pearse).

Genus *Cryptocreagris* Čurčić, 1984

Diagnosis.—Galea with apical branchlets. Abdominal sternites VI and VII each with 2 anterior discal setae. *Male genital area*: sternite II with a group of median and posterior setae, sternite III with a row of anterior, some intermediate and a series of posterior setae. *Female genital area*: sternite II with a group of small setae on each side of the midline, sternite III with a row of posterior setae.

Manducatory process with 4 setae. Femur and chelal palm of pedipalp with inconspicuous granulations. *Trichobothriotaxy*: *esb* distal to *eb*; *ist-isb-ib* clustered on finger base; *it* and *et* located distally on finger tip; *est* nearer to *it* than to *ist*; *st* slightly closer to *t* than to *sb*; *sb* slightly closer to *b* than to *st*.

Leg IV: tibia, basitarsus and telotarsus with one tactile seta each.

Type species.—*Microcreagris laudabilis* Hoff.

Subordinate taxa.—*Cryptocreagris laudabilis* (Hoff), *C. magna* (Banks).

Distribution.—California and New Mexico, USA.

Remarks.—In this study, the holotype and allotype of *C. laudabilis* have been restudied, in addition to the earlier redescription, based on the analysis of seven paratype specimens (Čurčić 1984).

Cryptocreagris laudabilis (Hoff)

Figs. 3, 4, 12, 13

Microcreagris laudabilis Hoff, 1956:4, 1958:12.

Diagnosis.—Epistome low and rounded apically, carapace with $4 + 6 + 4 + 4 + 6 = 24$ setae. Two pairs of eyes with flattened lenses. Galea with terminal branchlets. Flagellum with 8 anteriorly pinnate blades.

Tergites I-X with 6-9-11-12-12-12-13-17-17-15 (male) and 6-8-11-10-11-13-12-13-11-12 setae (female). *Male genital area*: sternite II with 27 median and posterior setae, sternite III with 5 anterior, 3 intermediate and 16 posterior setae, and 6 microsetae along each stigma. *Female genital area*: sternite II with a group of 4 small setae on either side of midline, sternite III with 12 posterior setae and 6 small setae along each stigma. Sternites VI and VII each with 2 anterior discal setae.

Pedipalps: fixed chelal finger with 71 (female) and 78 small and close-set teeth (male), distal teeth are asymmetrical, gradually changing from square-topped to eventually slightly asymmetrical teeth. Movable chelal finger with 72 (female) and 80 teeth (male), similar in form and size to those on the fixed chelal finger, but only few distal teeth asymmetrical.

Distribution.—New Mexico, USA.

Remarks.—In the holotype female of this species, two teratologies were noted. First, on the movable finger of the left chelicera, two galeal setae are developed (instead of one). Second, the right manducatory process bears 6 setae, while the left has the normal complement of 4 setae.

The material of *C. magna* has been redescribed elsewhere (Čurčić 1984).

Specimens examined.—Holotype male (C. Clayton Hoff 9152-S-2083.5) and allotype female (C. Clayton Hoff 9152-S-2083.9), under rocks, fir litter, near top of Mt. Taylor, Valencia Co., New Mexico, 11,150 ft. 21 July 1953.

Genus *Minicreagris* Čurčić, new genus

Name derivation.—Named for the small body size of its type species

Diagnosis.—Galea stylet-like. Flagellum of 7 or 8 blades, of which the proximal 3 are smooth and reduced in size from distal to proximal. *Male genital area*: sternite II with a group of median and posterior setae (of these, some setae are found along the posterior sternal margin), sternite III with a transverse row of some anterior and a series of posterior setae. *Female genital area*: one group of small setae on each side of the midline. Other abdominal sternites with one row of setae.

Manducatory process with 3 setae. Chelal palm of pedipalp with inconspicuous granulations (not "smooth" *sensu* Muchmore 1969). *Trichobothriotaxy*: *esb* distal to *eb*; *ib-ist-isb* in proximal part of finger; *est* closer to *it* than to *ist*; *sb*, equidistant from *st* and *b*; *st* somewhat closer to *t* than to *sb*, and closer to the interior finger margin (or teeth) than other trichobothria of the movable chelal finger.

Leg IV: tibia, basitarsus and telotarsus with one long tactile seta each.

Type species.—*Microcreagris pumila* Muchmore.

Subordinate taxon.—*Minicreagris pumila* (Muchmore).

Distribution.—Alabama and Tennessee, USA.

Remarks.—The study of the paratype male and paratype female of *M. pumila* (Čurčić 1984) has made me think that the taxonomic status of this species was debatable. The reason for this opinion was the inadequate number of males studied. The subsequent analysis of the holotype male has enabled me to reconsider *M. pumila* as the type species of a new genus. Its diagnostic characters include the number of eyes, the trichobothrial pattern, the setation of the manducatory process, the form and dermal structure of pedipalpal articles, the setation of the sternites and the form of flagellar blades. At present, *Minicreagris* is monotypic.

Minicreagris pumila (Muchmore), new combination

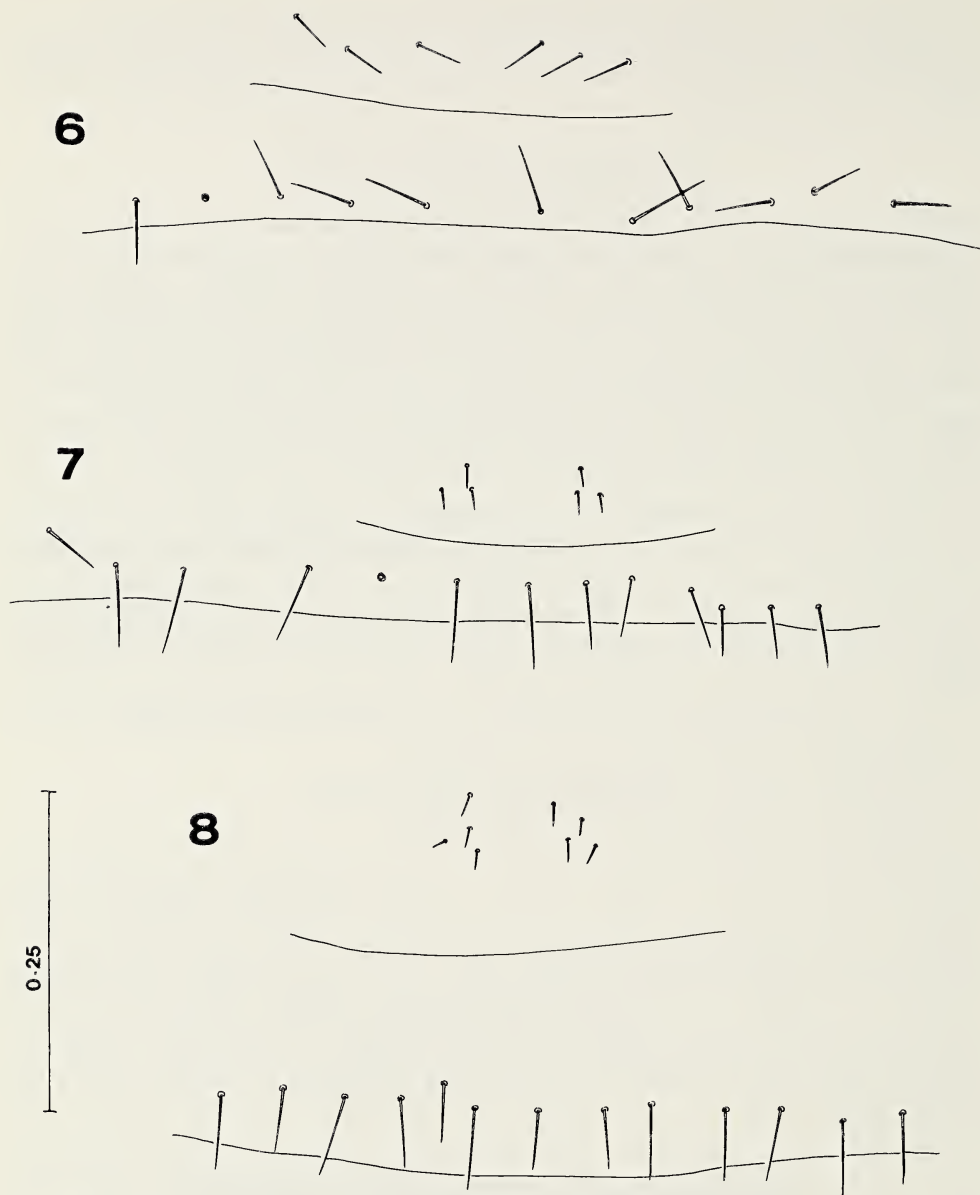
Figs. 5, 11

Microcreagris pumila Muchmore, 1969:2.

Diagnosis.—Epistome small and rounded. Carapace: 4 + 6 + 4 + 4 + 6 = 24 setae. With two small eyes. Galea simple.

Tergites I-X with 6-6-8-11-10-12-11-10-10-9 setae. *Male genital area*: sternite II with 10 setae. Of these, 6 are along the posterior sternal margin. Sternite III with 5 anterior and 10 posterior setae, and 3 suprastigmal setae on each side. Other sternites with one row of setae.

Pedipalps: fixed chelal finger with 43 small and close-set teeth, distal ones asymmetrical; proximal teeth rounded or slightly asymmetrical. Movable chelal



Figures 6-8.—Genital area: 6, *Alabamocreagris mortis* (Muchmore), holotype female; 7, *Australinocreagris reddelli* (Muchmore), holotype female; 8, *Australinocreagris texana* (Muchmore), holotype female. Scale in mm.

finger with 42 small and close-set teeth; distal teeth asymmetrically pointed, and proximal ones square-topped or rounded.

Distribution.—Alabama, Georgia, and (?) Tennessee, USA.

Remarks.—The descriptions of this species by Muchmore (1969) and by Čurčić (1984) define the species adequately, except for some details of the setation and dermal structure.

Muchmore (1969) suggested that this species is epigean and is only fortuitously collected in caves. That it may be widespread and more variable than indicated

by the same author is suggested by two other specimens from caves in Tennessee and Alabama.

Specimen examined.—Holotype male (WM 1009.01001), from Bryant Cave, Blount Co., Alabama, 19 March 1966 (S. Peck).

Genus *Alabamocreagris* Čurčić, 1984

Diagnosis.—Galea simple. Abdominal sternites uniseriate. *Male genital area*: sternite II with some median and posterior setae, sternite III with an anterior row of few setae and a posterior setal row. *Female genital area*: sternite II with a group of small setae on either side, sternite III with a transverse series of posterior setae.

Manducatory process with 4 long setae. Pedipalpal articles smooth, except for chelal palm which is inconspicuously granulate internally. *Trichobothriotaxy*: *esb* not distal to *eb*; *ist-isb-ib* at finger base; *it* and *et* located distally; *est* closer to *it* than to *ist*; *st* equidistant from *t* and *sb*; *sb* closer to *b* than to *st*.

Leg IV: tibia, basitarsus and telotarsus each with one or two tactile setae.

Type species.—*Microcreagris pecki* Muchmore.

Subordinate taxa.—*Alabamocreagris pecki* (Muchmore), *A. mortis* (Muchmore).

Remarks.—The type species has been described elsewhere (Čurčić 1984).

Alabamocreagris mortis (Muchmore), new combination
Figs. 6, 14

Microcreagris mortis Muchmore, 1969:8.

Diagnosis.—Epistome knob-like. Carapace with : 4 + 6 + 4 + 4 + 6 = 24 setae. Neither eyes nor eye-spots present. Galea unbranched.

Tergites I-X with 6-6-7-9-9-13-13-12-12-10 setae. *Female genital area*: sternite II with 3 small setae on either side of the middle, sternite III with 10 posterior setae and 3 suprastigmal microsetae on each side. Other sternites with single row of setae.

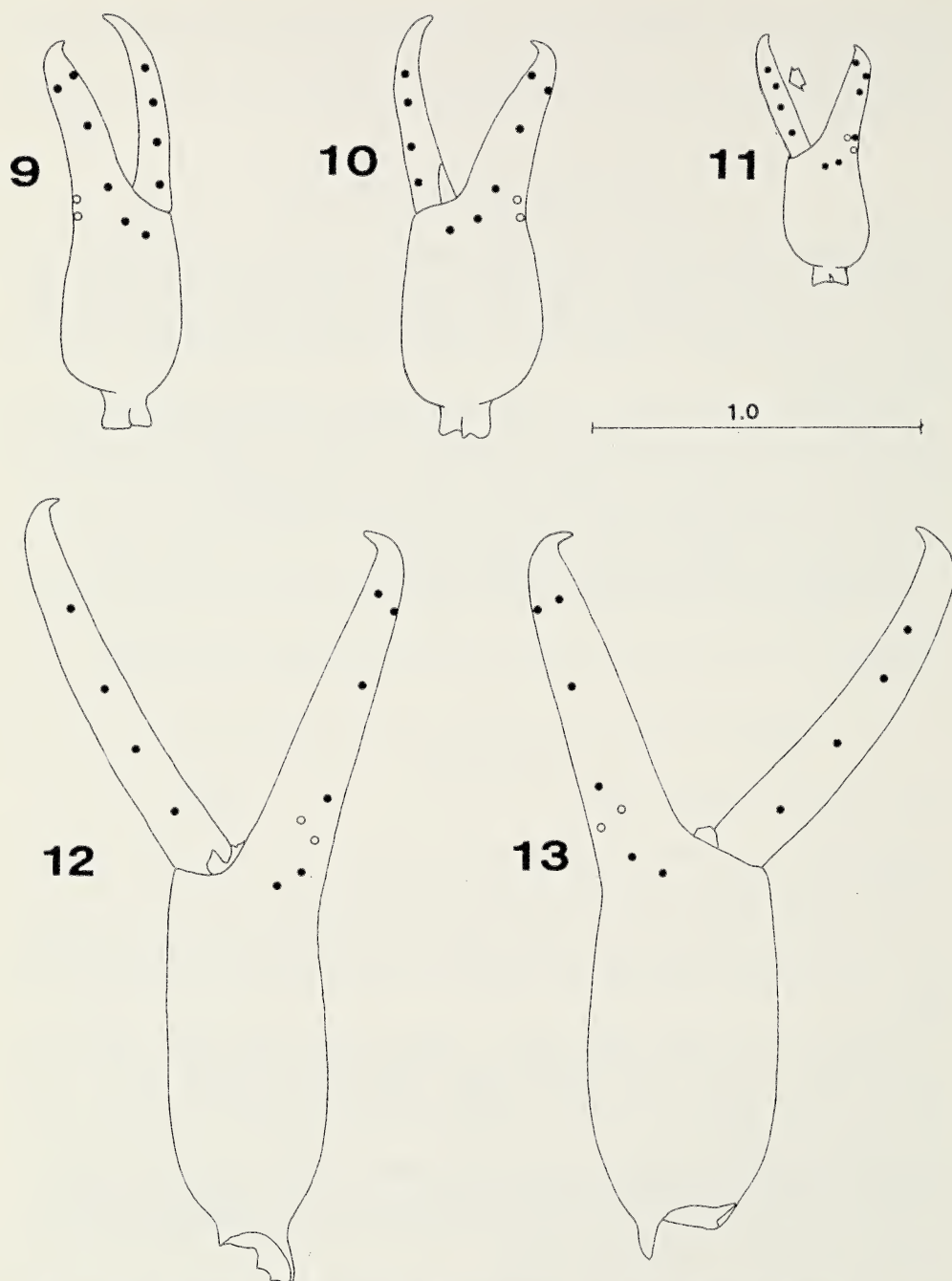
Pedipalps: fixed chelal finger with 71 close-set and small teeth, distal ones asymmetrical; proximal teeth square-topped. Movable chelal finger with 81 teeth which are small, close-set, distally asymmetrical, and rounded proximally; basal teeth square-topped.

Remarks.—*Alabamocreagris mortis* has a single tactile seta on telotarsus IV, whereas *A. pecki* bears two such setae.

Specimen examined.—Holotype female (WM 1555.01001), from "Morgue" Cave nr. Fern Cave, Jackson Co., Alabama, 22 June 1968 (W. Torode).

Genus *Australinocreagris* Čurčić, 1984

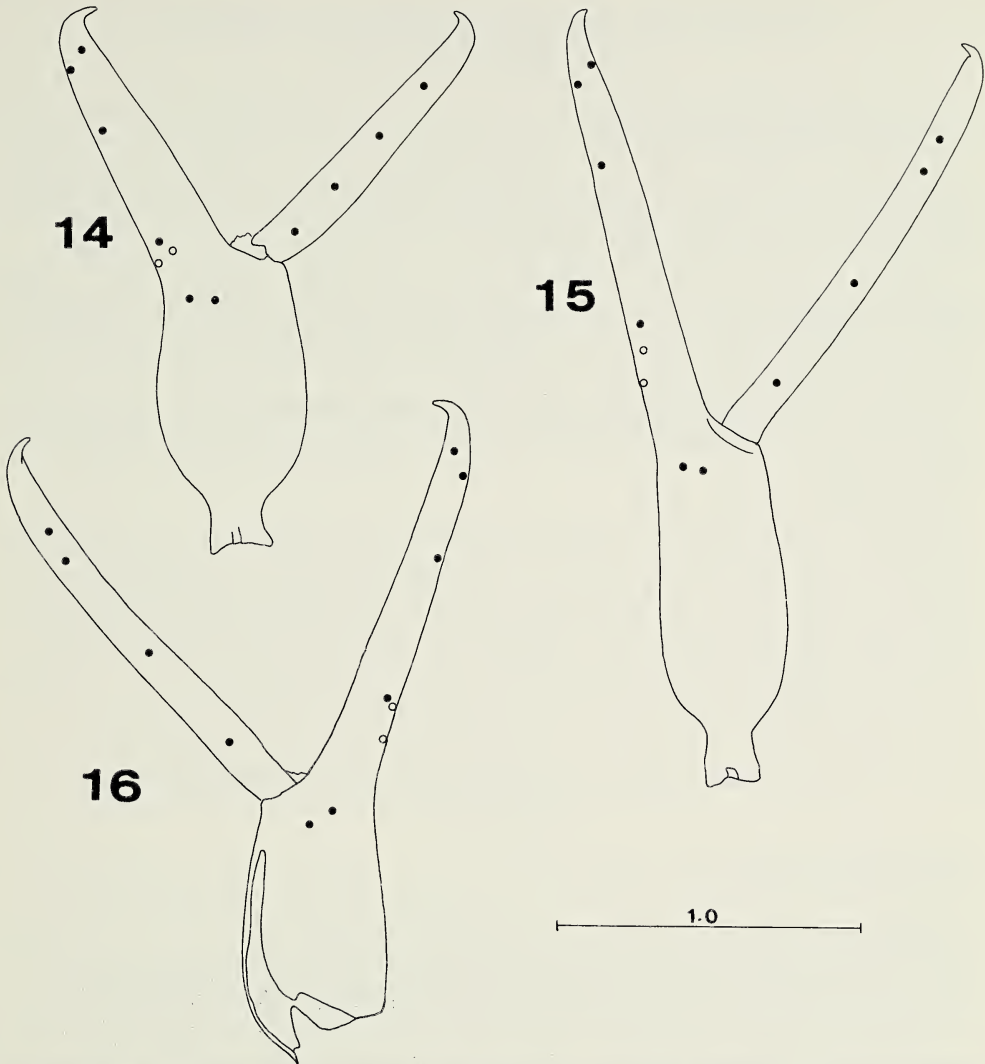
Diagnosis.—Galea simple, stylet-like, or branched apically. *Male genital area*: sternite II with a cluster of median and posterior setae, sternite III with a group of anterior and median setae, followed by few intermediary setae, and a transverse row of posterior setae. *Female genital area*: sternite II with a group of



Figures 9-13.—Trichobothrial pattern: 9, *Tuberocreagris lata* (Hoff), holotype male; 10, *T. lata* (Hoff), allotype female; 11, *Minicreagris pumila* (Muchmore), holotype male; 12, *Cryptocreagris laudabilis* (Hoff), holotype male; 13, *C. laudabilis* (Hoff), allotype female. Scale in mm.

small setae on either side of the middle, sternite III with a row of posterior setae. Abdominal sternites VI-VIII each with a pair of anterior discal setae.

Manducatory process with 3 (occasionally 4) setae. Pedipalpal articles inconspicuously granulate. *Trichobothriotaxy*: *esb* distal to *eb*, both setae on bulb of chela; *ist* and *isb* close to each other; *ib* somewhat closer to *ist* than to *esb*; *est*-



Figures 14-16.—Trichobothrial pattern: 14, *Alabamocreagris mortis* (Muchmore), holotype female; 15, *Australinocreagris texana* (Muchmore), holotype female; 16, *Australinocreagris reddelli* (Muchmore), holotype female. Scale in mm.

it-et in distal finger half; *st* closer to *t* than to *sb*; *sb* slightly closer to *st* than to *b*, or equidistant from these setae.

Tibia IV and basitarsus IV each with one long tactile seta, and telotarsus IV with one or two such setae.

Type species.—*Microcreagris grahami* Muchmore.

Subordinate taxa.—*Australinocreagris grahami* (Muchmore), *A. ozarkensis* (Hoff), *A. reddelli* (Muchmore), and *A. texana* (Muchmore).

Distribution.—Arkansas, California and Texas, USA.

Remarks.—In the description of *Australinocreagris*, Čurčić (1984) erroneously stated that sternite III of the male is beset with “few intermediary setae”. Actually this sternite has only a small group of anterior and median setae and a transverse row of posterior setae, as illustrated in fig. 7 of the same paper.

Australinocreagris reddelli (Muchmore), new combination

Figs. 7, 16

Microcreagris reddelli Muchmore, 1969:17.

Diagnosis.—Epistome absent. Carapace with $4 + 6 + 2 + 5 + 4 = 21$ setae. Neither eyes nor eyespots developed. Both galeae broken and lost. Flagellum eight-bladed, all blades pinnate anteriorly.

Tergites I-X with 8-10-12-11-11-12-11-11-9 setae. *Female genital area*: sternite II with a small group of 3 setae on either side of the midline, sternite III with 13 posterior setae and 6 microsetae along each stigma. *Male genital area*: unknown. Sternites VI-VIII each with a pair of anterior discal setae.

Pedipalps: fixed chelal finger with 85 small and close-set, asymmetrically pointed teeth. Movable chelal finger with 98 small, asymmetrically pointed and close-set teeth.

Distribution.—Texas, USA.

Remarks.—In this species, basitarsus IV has two tactile setae. In view of the fact that *A. texana* has one such seta on this podomere, it is probable that the number of tactile setae on basitarsus IV reflects intrageneric variability, just as is seen in the members of the genus *Neobisium* Chamberlin, 1930 (Čurčić 1982b).

Specimen examined.—Holotype female (WM 171.01001), under small rock on silt in darkness, Shultz Cave, 2 miles E Valente, Travis Co. Texas, 21 August 1963 (Bill Russell).

Australinocreagris texana (Muchmore), new combination

Figs. 8, 15

Microcreagris texana Muchmore, 1969:18.

Diagnosis.—Epistome minute and knob-like. Carapace with $4 + 6 + 7 + 6 = 23$ setae. Neither eyes nor eye-spots present. Galea biramous, each ramus with 2 or 3 terminal branchlets. Flagellum nine-bladed, all blades pinnate anteriorly.

Tergites I-X with 8-8-12-14-13-14-13-12-13-10 setae. *Female genital area*: sternite II with 4 small setae on each side of the midline, sternite III with a series of 13 posterior setae and 6-8 small setae along each stigma. *Male genital area*: unknown. Sternites VI-VIII each with a pair of anterior discal setae. Even on sternite IX two median setae are found slightly anterior to posterior setal row.

Pedipalps: fixed chelal finger with 99 low, close-set and small teeth; distal ones asymmetrically pointed and proximal ones square-topped but still slightly asymmetrical. Movable chelal finger with 108 teeth of the same form and size as those on the fixed finger.

Distribution.—Texas, USA.

Remarks.—This species has one tactile seta on telotarsus IV, and *A. reddelli* has two such setae. Until more examples are available, the occurrence of the different number of tactile setae on telotarsus IV in the members of *Australinocreagris* may be regarded as the case of intrageneric variability.

Specimen examined.—Holotype female (WM 849.01001), from Tooth Cave, Travis Co., Texas, 16 May 1965 (T. Barr, R. Mitchell, W. Andrews).

Key to *Microcreagris*-related Genera of North
American Pseudoscorpions

The newly established genus and its related genera (Čurčić 1984) may be distinguished by means of the following key:

1. Some abdominal sternites with two rows of setae 2
Abdominal sternites with one row of setae 5
2. Sternites VI and VII with two rows of setae *Cryptocreagris* Čurčić
Sternites VI-VIII with two rows of setae 3
3. Sternite III of the female with a transverse row of posterior setae 4
Sternite III of female with a transverse row of posterior setae and a few
setae on face near middle *Tartarocreagris* Čurčić
4. Sternite II of female with a group of setae on either side of midline.
Manducatory process with 3 setae *Australinocreagris* Čurčić
Sternite II of female with a unique group of setae in the form of an inverted
"U". Manducatory process with 4 setae *Saetigerocreagris* Čurčić
5. Sternite III of male with an anteromedian groove in the form of a "V",
bordered by two pairs of small setae *Fissilicreagris* Čurčić
Sternite III of male with an ungrooved anterior margin: anterior setae
clustered or arranged in a row 6
6. Pedipalpal articles smooth *Lissocreagris* Čurčić
Some pedipalpal articles granulate 7
7. Chelal trichobothria *sb* and *st* equidistant from *b* and *t* respectively 8
Chelal trichobothrium *sb* closer to *b* than to *st*, or somewhat closer to *st*
than to *b* 9
8. Manducatory process with 3 long setae. Pedipalpal femur granulate, femur
and tibia with one and two accessory tubercles respectively
..... *Tuberoocreagris* Čurčić
Manducatory process with 4 long setae. Pedipalpal femur and tibia
smooth *Alabamocreagris* Čurčić
9. Chelal trichobothrium *st* somewhat closer to the interior finger margin than
are *sb* or *b* *Minicreagris*, new genus
Chelal trichobothrium *st* as close to the interior finger margin as *sb* or *b*
..... 10
10. Sternite III of male with a cluster of anteromedian setae and a row of
posterior setae *Americocreagris* Čurčić
Sternite III of male with an anteromedian group of setae, a series of
intermediary setae and a transverse row of posterior setae
..... *Globocreagris* Čurčić

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I am grateful to the reviewers, W. B. Muchmore and Vincent F. Lee for the constructive criticism and valuable comments on the problem studied. I am also indebted to Norman Platnick of the American Museum of Natural History in New York for the loan of the type specimens considered herein.

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RESEARCH NOTES

**A NEW SPIDER, *PARATHEUMA MAKAI*
(ARANEAE, DESIDAE), FROM HAWAII**

In two previous papers (Beatty and Berry 1988a, 1988b) we dealt with the seven known species of the desid genus *Paratheuma* Bryant, and we suggested that the discovery of additional species might be expected. One such species was subsequently collected on two of the Hawaiian Islands and is described here.

The specimens occurred on rocky ocean beaches, as is characteristic for the genus; but the Hawaiian beaches, in contrast to many other localities where *Paratheuma* occurs, were almost devoid of broken coral. Instead, a dark, smooth heavy volcanic rock (probably basalt) (Fig. 1) or abrasive lava was common. On Kauai the spiders were found on the sand under basalt rocks varying from about 10-50 cm in diameter. On Hawaii they were on sand in the spaces between smaller pieces of rough porous lava.

Four adults of each sex were measured. Total length was measured from anterior carapace margin (or anterior eye margin when eyes projected beyond carapace) to the base of the spinnerets. Some specimens from Kauai were reared



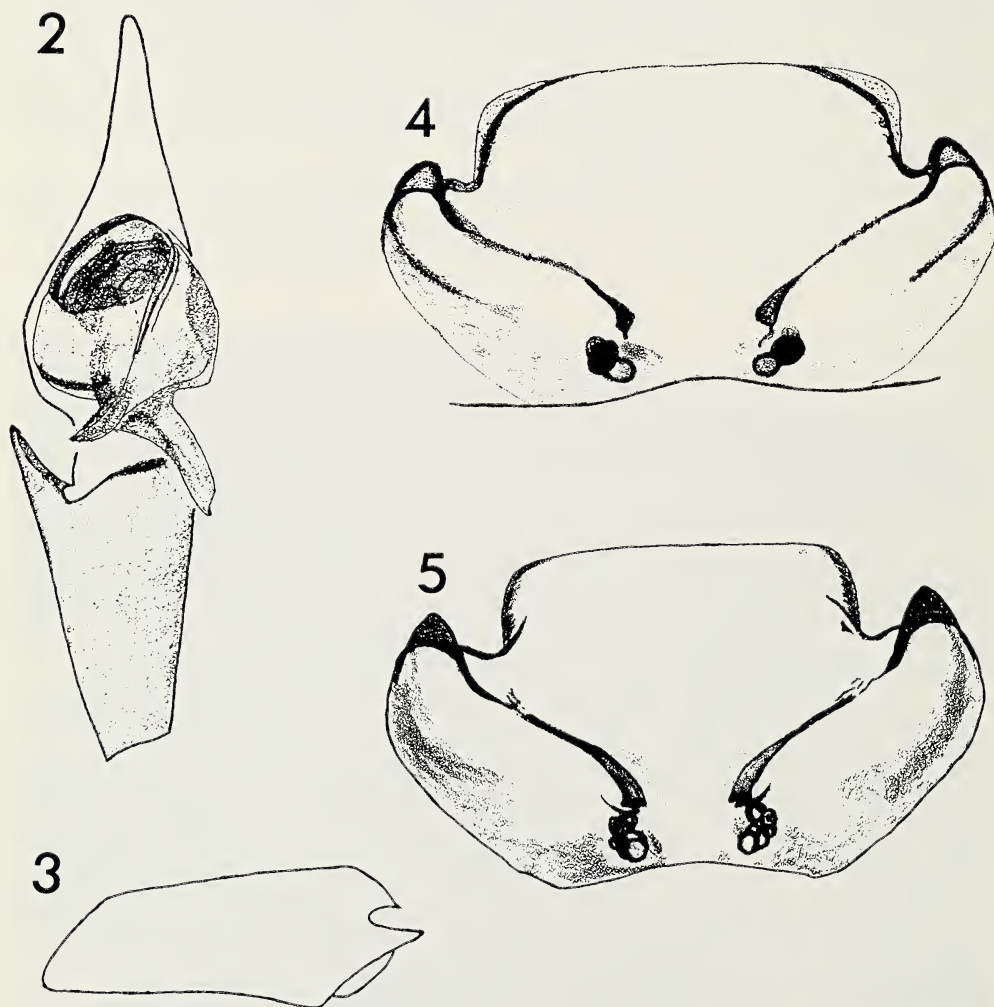
Figure 1.—Type locality of *Paratheuma makai*, beach at Kapaa, Kauai, Hawaii.

in the laboratory but are not listed below. Juveniles listed here are not considered paratypes.

Paratheuma makai, new species

Holotype.—Male from Hawaii; Kauai Island, at mile marker 9.4 N of Kapaa, under beach rocks, 14 Jan. 1988 (J. W. and E. R. Berry) in Bishop Museum, Honolulu, Hawaii. The name, regarded as a noun in apposition, is a Hawaiian word meaning "toward the ocean".

Diagnosis.—Male with relatively short (length less than twice basal width), erect, almost triangular tibial apophysis, and long arcuate retrolateral branch of conductor tip. Female with epigynal depressions curved slightly forward anteriorly, the hoods flanked medially by distinct notch-like depressions. Similar to *P. australis* Beatty and Berry, *P. insulana* (Banks), and *P. rangiroa* Beatty and Berry, but clearly distinguished from them by the characteristics cited.



Figures 2-5.—Genitalia of *Paratheuma makai*: 2, left pedipalp, ventral; 3, tibia of left pedipalp, lateral; 4, epigynum, ventral; 5, epigynum, dorsal, cleared.

Descriptive notes.—*Male*: Total length 3.3–4.0 mm, carapace length 1.7–1.9 mm, maximum carapace width 1.26–1.32 mm. Embolus arising on medial side of bulb near middle of bulb's length, its structure as in other species of the genus. End of conductor with short medially directed branch and long arcuate retrolateral branch curving down over distal retrolateral surface of tibia (Fig. 2). Tibial apophysis erect, shorter than in any other species except *P. interaesta* (Roth and Brown), triangular, its length less than twice its basal width (Fig. 3). Bristle pattern as in other Pacific species.

Female: Total length 3.5–4.3 mm, carapace length 1.6–1.7 mm, maximum carapace width 1.08–1.26 mm. Epigynal depressions pale, extending obliquely forward, arching slightly mediad at anterior ends. Epigynal hoods distinct, flanked medially by depressions. Anterior border of epigynum broadly rectangular (Fig. 4). Ducts of epigynum narrow, twisted tightly around themselves so that their course is very difficult to determine (Fig. 5). Seminal receptacle and duct complex smaller than in other Pacific species.

Discussion.—Many localities on Kauai were searched, but the spiders were found only at the beach at Kapaa, where they were abundant. No specimens were found on Oahu, and few on Hawaii. However, only a small portion of Hawaii's beach was searched.

Specimens from Hawaii were smaller than the mean for specimens from Kauai; but only one adult of each sex was taken on Hawaii, and the male matured in the laboratory. In all other characters they agreed with the Kauai specimens. Genitalic structure in both sexes is most similar to those of *P. australis* and *P. rangiroa*, and somewhat less to *P. insulana*. Other structures are almost uniform throughout the genus.

This species conforms to the distribution pattern shown by other species of the genus—only one species of *Paratheuma* on any given island, although a given species may occur on more than one island or island group. Further investigation is needed to confirm this pattern and to determine the total area occupied by the genus. Islands in need of investigation are those in Polynesia east and south of Rangiroa and Manihi, and in Melanesia, Indian Ocean and the Atlantic Ocean.

Distribution.—**HAWAII:** Kauai and Hawaii Islands.

Specimens examined.—**HAWAII:** *Kauai Island*, under beach rocks at mile marker 9.4 N of Kapaa, 14 Jan. 1988 (J. W. and E. R. Berry), 7 males, 5 females, 4 immatures. *Hawaii Island*, in lava on beach, 25 road miles NW of Kailua at Anaehoomalu, 18 Jan. 1988 (J. W. and E. R. Berry), 1 male, 1 female, 2 immatures.

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PREY OF THE CRIBELLATE SPIDER, *DICTYNA ANNULIPES* (ARANEAE, DICTYNIDAE), ON APPLE TREE FOLIAGE

Cribellate spiders belonging to the genus *Dictyna* are often abundant on the foliage of fruit trees and other plants where they spin their webs on the upper surface of partially rolled leaves, in the axils of twigs and on the bark (Chant 1956; Putman 1967; McCaffrey and Horsburgh 1980; Temerak 1981; Nuessly and Golden 1983; Bostanian et al. 1984). Putman (1967) reported that *D. annulipes* (Blackwall) was a common spider on peach bark, and also recovered *D. foliacea* (Hentz) and *D. sublata* (Hentz) by limb jarring.

In 1988, *D. annulipes* was the predominant spider (76.2%, $N = 235$ spiders) on the foliage of dwarf apple trees, cultivars McIntosh and Empire, at Jordan Station, Ontario. To assess the importance of this spider as a general predator in apple orchards, determination of its prey was undertaken by analysis of carcasses in its web and by assays of gut contents by immunoelectroosmophoresis as described by Allen and Hagley (1982). Webs (\bar{x} no. per tree = 32, $N = 7$ trees) were examined at two- to three-day intervals and prey carcasses identified *in situ*, or the webs removed and examined microscopically in the laboratory. Spiders removed from the webs were placed individually in No. 000 gelatin capsules and frozen (-15°C) immediately. Serological tests were subsequently performed on individual spiders to determine if they had fed on insects in the orders Diptera, Hemiptera/Homoptera, Hymenoptera and Lepidoptera using antisera prepared to the apple maggot, *Rhagoletis pomonella* (Walsh), the green apple aphid, *Aphis pomi* DeGeer, the braconid, *Pholetesor ornigis* (Weed) and the leafminer, *Phyllonorycter blancardella* (Fabr.), respectively.

Chironomids (Diptera), (species undetermined), were the major prey (70.7%, $N = 222$ prey cadavers) of *D. annulipes* as determined by web analysis. Putman (1967) also suggested that chironomids were the major prey of web-spinning spiders, including *Dictyna* spp., on peach trees. The second largest group of prey were Hemiptera/Homoptera (15.3%) of which the leafhopper, *Typhlocyba pomaria* McAtee (5.88%) and the mirid, *Campylomma verbasci* (Meyer) (5.0%) were the most frequently recovered species. Chant (1956) reported that *D. arundinacea* L. fed on the mirid, *Plagiognathus arbustorum* Fab., but the anthocorid, *Anthocoris nemorum* L., was rejected. Chant (1956) also stated that aphids and coccids were not particularly favored by *D. arundinacea*. *Dictyna annulipes* apparently did not favor the green apple aphid, *A. pomi*, which comprised only 2.7% of the prey in the webs. Although McCaffrey and Horsburgh (1980) did not analyse the contents of the webs of *D. foliacea* and *D. sublata*, they suggested that the webs would be most effective for the capture of small, weak-flying insects, such as leafhoppers and aphids.

Other groups of prey in the webs of *D. annulipes* included Araneae (4.5%), Hymenoptera (2.7%), Lepidoptera (1.8%), Neuroptera (0.9%) and other Diptera (4.5%).

The proportion of *D. annulipes* giving positive serological reactions for various prey groups is shown in Table 1. The greatest proportion of spiders tested positive for the Hemiptera/Homoptera group. The number of spiders that were serologically positive to the antisera for Diptera decreased from May through

Table 1.—The proportion ($N = 177$) of *D. annulipes* that were serologically-positive for four prey groups.

Month	No. <i>D. annulipes</i> tested	Diptera	Hemiptera/ Homoptera	Hymenoptera	Lepidoptera
May	24	12.5	41.7	8.3	8.3
June	89	9.0	36.0	16.9	19.1
July	33	6.1	39.4	30.3	15.2
August	31	1.2	14.3	13.0	31.2

August, probably due to the fact that chironomids were most abundant in late April and May (unpublished data). Chironomid carcasses accumulated in the webs over time, as they were not removed by *D. annulipes*. Feeding on Hymenoptera and Lepidoptera increased as the season progressed and probably reflects an increase in the density and activity of both predator and prey (unpublished data). Of 177 *D. annulipes* that had fed, 75.7% consumed individuals of one prey group, 20.9% of two prey groups and 3.4% of three prey groups.

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**OBSERVATIONS ON THE SOCIAL SPIDER,
ANELOSIMUS DOMINGO (ARANEAE, THERIDIIDAE),
IN SOUTHWESTERN PERU**

Although *Anelosimus domingo* Levi (Araneae, Theridiidae) was described in 1963 (Levi 1963), little is known about its natural history. It is now evident that *Anelosimus saramacca* Levi and Smith (1982) is a synonym of *A. domingo* Levi (1963). (NEW SYNONYMY: Levi, per. comm.). Levi and Smith (1982) mention that the species is cooperatively social and include some habitat features in their description. Here we intend to definitively document the cooperative foraging in this species and report some preliminary observations of its web structure and behavior patterns in relation to other *Anelosimus* species.

In 1987 and 1988 we discovered a total of five communal webs of *A. domingo* in the forest undergrowth vegetation of the Tambopata Reserved Zone (12°50'S, 069°17'W), Madre de Dios, Peru. This 5,500 hectare reserve consists of pristine Amazonian forest on the border between the Tropical and Subtropical Zones as classified by Holdridge et al. (1971). All of the *A. domingo* webs that we found were located in the upper flood plain forest type at Tambopata. This forest type is created by flooding that occurs periodically in certain areas of the Amazon basin creating a secondary flood plain with soils richer than upland forest (Erwin 1984). This habitat, which has a very diverse plant community, is dominated by palms (*Iriartea*) of medium height (25-35 m tall). Each web was positioned in the undergrowth such that it was exposed to direct sunlight from zero to a maximum of three hours each day. *A. eximius* appears to have a much broader habitat range as we found its webs in five of the seven forest types described at Tambopata as well as along lagoons and paths where they could be exposed to sunlight 6 or 7 hours in a day. Another social species in the same genus found at Tambopata, *A. rupununi*, was only found in clearing areas or along bodies of water where they were exposed to direct sunlight nearly all day (pers. observ.). We found the first two webs of *A. domingo* in June 1987 and observed them periodically between that time and August 1988. By July 1988, one of those webs had deteriorated and disappeared and we had found three additional webs. Webs were isolated and uncommon even within the appropriate forest type (smallest nearest neighbor distance was 2.5 km).

The appearance of *A. domingo* webs is very similar to that of *A. eximius* (see Brach 1975; Vollrath 1982; Christenson 1984 for descriptions of *A. eximius* webs). All of the webs we found consisted of a single basket-shaped sheet of webbing with dead leaves and adjacent vegetation incorporated as retreats. Above this sheet was a non-sticky tangle of barrier webbing that can extend into neighboring vegetation several meters (Table 1). We estimate that there were several hundred individuals housed in each web, however, at any moment in time, only about 20-40 spiders were distributed in obvious areas (Table 1). The rest of the spiders were in retreats under leaves where many of them were situated in such a way that they could efficiently respond to prey or other disturbances in the web. Also in these retreats some adult females would be guarding egg sacs and caring for very young juveniles. Because it was difficult to see into the retreats in the *A. domingo* webs, we were unable to determine if females fed spiderlings by

Table 1.—Measurements in cm of *A. domingo* webs. Sheet measurements represent the length, width and depth of that basket-shaped structure. The height of the web is given as the lowest point of the sheet. The barrier extends up from the sheet into vegetation.

Web	Sheet	Height	Barrier	# Spiders visible (mean \pm SD)
1	80 \times 81 \times 22	40	200	32.5 \pm 11.3
2	65 \times 70 \times 40	70	140	27.5 \pm 5.5
3	41 \times 38 \times 15	32	79	21.4 \pm 12.3
4	110 \times 140 \times 35	12	290	39.3 \pm 18.3
5	22 \times 18 \times 10	84	45	11.3 \pm 6.1

regurgitation in a manner similar to *A. eximius* (Christenson 1986 and pers. observ.).

Just as for *A. eximius* (Nentwig 1985), the cooperative behavior and large webs constructed by *A. domingo* enables them to capture prey many times their own body size and mass (Table 2). The prey capture sequence is virtually identical to that we have observed in a sympatric population of *A. eximius*. When an insect enters the web several spiders emerge and begin to subdue the insect by circling and wrapping it with silk. Periodically individuals will move in and bite until the insect is killed. Although not significant with our small sample size, it appears that a larger number of spiders react in a shorter period of time to larger prey (Table 2). It took more individuals of *A. domingo* significantly longer to subdue large prey items (35-40 mm in length) in comparison to smaller prey (5-15 mm in length) (Mann Whitney *U*-test, $p < 0.05$) (Table 2). If the insect is relatively small it is moved from an exposed area of the web to one of the more protected retreats where spiders in all age classes can feed. Larger insects are left in the lower portion of the barrier web and the spiders emerge from retreats to feed on them there.

Interspecific tolerance and even interspecific cooperation have been reported for other social spider species (Fowler and Levi 1979; Krafft 1970, 1975). We found, however, that *A. domingo* and *A. eximius* are not tolerant of one another. Adult females of *A. eximius* did not survive when introduced into the field webs of *A. domingo*, although we were very successful at introducing spiders into different colonies of the same species. Six laboratory experiments were conducted in which one female of each species (matched by size) was introduced into a six-dram vial measuring 2.5 \times 4.5 cm (3-6 spiders of a single species lived well for extended periods of time in vials of this size). In two experiments we introduced the spider at the same time. In the first vial, the *A. domingo* had attacked the *A. eximius* within the first five minutes and they had five aggressive interactions

Table 2.—Number of spiders and duration of the reaction period and handling time of prey items introduced into *A. domingo* webs (mean \pm SD). a = Values for largest prey size are significantly different from values for smaller categories by Mann-Whitney *U*-test ($P < 0.05$).

Prey size	<i>N</i>	Reaction time (sec)	Number of spiders reacting	Handling time (sec) ^a	Number of spiders handling ^a
5-10 mm	4	0.6 \pm 0.5	3.1 \pm 1.2	201 \pm 91	2.3 \pm 3.3
10-15 mm	5	0.3 \pm 0.5	3.3 \pm 1.3	375 \pm 158	4.0 \pm 8.2
35-40 mm	4	0.2 \pm 0.7	7.1 \pm 5.2	982 \pm 315	10.1 \pm 3.2

within an hour. That female *A. domingo* killed the *A. eximius* in the third day. In the other vial no activity was observed and, by the third day, the two spiders had divided the space approximately equally with one spider at each end. In four other vials we introduced one female first and allowed her 24 hours to establish a small web inside the vial before we introduced the female of the other species. Two vials received *A. domingo* first and two vials received *A. eximius* first. The results of these experiments were symmetrical. Of the two vials in which *A. domingo* established webbing prior to *A. eximius*, one ended up with a single *A. domingo* and the other ended up with a single *A. eximius* after three days. The outcome was identical for the vials in which *A. eximius* was introduced first. The results of these experiments indicate that *A. domingo* and *A. eximius* will not coexist peacefully or cooperate with one another. It is apparent, however, that these species are capable of using one another's web. Also there appears to be no home bias among these spiders. That is, the spider spinning the initial web had no advantage in the contests we set up.

The observations we have made firmly places *A. domingo* among the cooperatively social spiders of the genus. Because sociality is well-developed among *Anelosimus* spiders, comparative studies of all aspects of their biology become important to our understanding of the evolution of social behavior both within this genus and in other spiders as well. Certainly more detailed investigations of *A. domingo* will help us understand some of the ecological factors that influence the evolution of social behavior.

We would like to thank K. R. Cangialosi, G. J. Binford, J. L. Whitis, D. Silva and K. Renton for assistance in the field. J. Coddington offered advice and suggestions as well as identifying the spiders for us. H. W. Levi, T. E. Christenson and W. Nentwig offered valuable suggestions on an earlier draft of this note. Specimens were deposited at the National Museum of Natural History, Smithsonian Institution. This research was supported by NSF grant BSR-8604782, by the Hamilton Campus of Miami University and by the Department of Zoology, Miami University, Oxford Campus.

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**EGG PREDATION BY *CATOLACCUS* PROB. N. SP.
(HYMENOPTERA, PTEROMALIDAE) ON THE SPIDER,
DICTYNA COLORADENSIS (DICTYNIDAE)**

This note documents predation by the wasp, *Catolaccus* prob. n. sp. on the eggs of *Dictyna coloradensis* Chamberlin in northern Idaho and eastern Washington. Egg sacs of *D. coloradensis* were collected from the rangeland weeds, spotted knapweed (*Centaurea maculosa* Lamarck) and yellow starthistle (*C. solstitialis* L.) (Asteraceae). One or the other of these plant species dominated each collection site (see below). Web height, when collected from spotted knapweed and yellow starthistle, were an average of (\pm SE) 64.7 (\pm 7.2, $n = 18$) and 39.2 (\pm 2.8, $n = 36$) cm, respectively. In spotted knapweed, the webs were found in the stems, whereas in yellow starthistle they were located among the flower spines.

Collections were made in three areas: (1) north Idaho panhandle (Farragut State Park [8.3 km E of Athol] and Athol [1.6 km E of Athol] sites; Kootenai Co.) where spotted knapweed comprised the primary web substrate; (2) eastern Washington (Chief Timothy State Park [8.3 km W of Clarkston]; Asotin Co.) and (3) north central Idaho (the Pond [5.1 km NW of Culdesac] and Central Grade [6.4 km NE Hatwai] sites; Nez Perce Co.) where egg sacs were collected from yellow starthistle substrates. Twenty webs were collected ca. weekly from May through September and egg sacs present were examined for the presence of the wasp.

Dictyna coloradensis egg sacs collected at various sites were found to be infested with a predacious pteromalid, *Catolaccus* prob. n. sp. (based on the taxonomic determination by Eric E. Grissell). Larvae of this pteromalid were found feeding upon eggs within the egg sac. When an egg sac was infested, all eggs were consumed by a single pteromalid larva. Although the pteromalid eggs were never found, they were either layed singly or multiple ovipositions resulted in the mortality of all but one individual as only a single pteromalid adult was reared from all parasitized egg sacs.

The spider egg sacs were flocculent white, constructed of dense silk and always attached adjacent to the web retreat in the center of the hackled-band, mesh web. No external evidence of parasitism could be identified on the web or egg sacs,

thus we suspect wasp eggs were laid within the egg sac by the thin wasp ovipositor (ca. 1 mm long).

Most species of *Catolaccus* are secondary parasites of ichneumonid or braconid parasites of Lepidoptera or Coleoptera (Burks 1954). We found no other records of spider egg predation by members of this genus. Another pteromalid, *Arachnopteromalus dasys* Gordh, has been reported as an egg sac parasite (= egg predator) of several uloborid spider species (Gordh 1976, 1983; Peaslee and Peck 1983); thus, predation of cribellate spider eggs by pteromalids may have evolved more than once along independent lineages (G. Gordh, pers. comm.).

The percent parasitism of egg sacs collected at the different sites during 1982 were: Athol, 19% ($n = 183$); Farragut State Park, 23% ($n = 13$); Chief Timothy State Park, 24% ($n = 17$); and 0% ($n = 49$) at the Pond site. During the 1983 season, for unknown reasons, the percent parasitism dropped dramatically: Farragut State Park, 7% ($n = 84$); Central Grade, 0% ($n = 26$); and the Pond site, 0% ($n = 22$). Percent parasitism over the sites was 16% ($n = 262$) during 1982 and 5% ($n = 132$) during 1983. Wasp parasitism of 2 and 3 egg sacs located in single webs occurred three times each. *Dictyna coloradensis* females produce an average of 2-3 egg sacs (Wheeler 1985); thus, when attack occurs, egg predation may significantly reduce reproductive success of this spider. However, the cause(s) of the decline in parasitism rates (e.g., weather, defensive response, alternate hosts) between the two years is yet unknown.

Adult wasps were occasionally observed alighting and walking freely on *D. coloradensis* webs in the laboratory and in the field, apparently without provoking the spider. The pteromalid was never found ensnared in the spider webs. Field observations of *D. coloradensis* indicate that the adult females remain in the web with the eggs and the first two instars until spiderling dispersal, perhaps to assist in prey capture or to guard the offspring against natural enemies (Wheeler 1985). On two occasions ants entering the webs of mature females were confronted with apparently defensive charging and web tugging by the spider. After 5 min of observation in both cases, a standoff resulted where neither the ants nor the spiders appeared to gain an advantage. However, based upon our wasp observations, protection from this egg predator may be ineffective due to wasp adaptations for walking freely on webs and the lack of spider defensive responses to wasp infestation.

Gratitude is extended to W. J. Gertsch and E. E. Grissell for determination of the spider and pteromalid species, respectively. Gordon Gordh provided additional taxonomic assistance with the pteromalid. Wasp and spider specimens are deposited in the W. F. Barr museum, University of Idaho. Financial support was provided, in part, by a grant (USDA-ARS, Fed. Grant #58-91H2-4-0007) awarded to R. H. Callihan and J. B. Johnson and Idaho Agricultural Experiment Station Project 061-R838 (J. P. McCaffrey), a contributing project to Western Regional Project, W-84. This is University of Idaho Agricultural Experiment Station Publication number 8976. We appreciate the critical reviews of earlier drafts of this manuscript by James B. Johnson and Dennis J. Schotzko.

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BOOK REVIEWS

Ono, Hirotugu. 1988. A Revisional Study of the Spider Family Thomisidae (Arachnida, Araneae) of Japan. National Science Museum, Ueno Park 7-20, Tokyo 110, Japan (Unpriced).

This is a coherent and critical treatment of the Thomisidae found in Japan. Based on a solid background of painstaking genus-by-genus revisionary work extending over the past nine years, the book provides workers with the taxonomic knowledge needed to identify 22 genera and 53 species of Japanese crab spiders. It is noteworthy that Ono has studied material and literature from regions beyond the confines of his own country, thus presenting a broad treatment that will interest arachnologists the world over.

On opening the book the reader is greeted by three strikingly beautiful color photographs. One shows *Xysticus croceus* with its fangs buried in the thorax of a lycaenid butterfly, another a pair of *Oxytate striatipes* suspended in copula on a thread. The body of the book is illustrated with high-quality line and stipple drawings showing the habitus, the male palpus in two views, and the epigynum in external and internal views. These are supplemented by a table of anatomical terms which Ono uses in a sense different from that of other workers. The range maps show only collection localities within the country itself, though range statements give the world distribution. There is no attempt to illustrate intraspecific variation. For illustrations of eight of the species the reader is referred to earlier papers by Ono.

The descriptions and synonymies are quite full. The inclusion of *nomina nuda* is a dubious practice, however, and there are no references to the world catalogues of Bonnet, Roewer, Brignoli, or Platnick. There are many new synonyms based on examination of types or of presumably reliable publications. Ono gives leg setal placement in great detail, though based on single specimens, and no use is made of these in keys or diagnoses. Measurements are given as simple ranges of values with no indication of sample size; a mean and standard deviation are preferable, as these enable users of the book to make decisions about size differences. The biological notes on each species are useful.

The approach to the problem of intergrading genera is interesting. For example, the assemblages known under the names *Xysticus* (with 350 described world species) and *Coriarachne* (with only six) if distinguished in the usual way leave some species that do not fit very well. Ono's solution is to interpose a third genus, *Bassaniana*, for some of the intermediates, based on relative degree of body flattening and relative lengths of the third and fourth pairs of legs. Thus the East Asiatic *Coriarachne decorata* sits uneasily with the North American *C. versicolor*, *C. utahensis*, and *C. floridana* in *Bassaniana*, and the European *C. depressa* with some *Xysticus* spp. in *Coriarachne*. As expected, it becomes more difficult to distinguish the three genera than the two. The characters are subject to exceptions, and for some species the character has never been made known. Such a classification needs more work to make it endure.

Ono proposes the Clubionoidea, or part thereof, as sister group of the Thomisidae. He recognizes the heterogeneity of the clubionoids. The most primitive subfamily of thomisids is thought to be the Stephanopinae, and the most specialized the ant mimics of the subfamily Aphantochilinae. The synapomorphy for Thomisidae is the ambush type of prey capture, which arose with the exaggerated development of the first two pairs of legs as a powerful grappling device. Members of the family also share an unusual development of the anterior lateral eyes and diurnal hunting behavior. The most speciose subfamily in Japan, as in the world, is the Thomisinae, with 17 genera and 44 species. Ono provides an arrangement of the world thomisine genera into 13 tribes, but without characters to distinguish them.

The island chain forming Japan extends approximately from latitude 25° to 45° north, and experiences climates from the humid subtropics to the cold temperate. In an interesting section at the end of the book, the author speculates on the origins of the Japanese thomisids. The majority of species are thought to represent the Old World tropics, several of which have spawned Japanese endemics. *Xysticus daisetsuzanus* is quite unique, being found only on Mt. Daisetsu-zan in central Hokkaido and having its closest relatives in the circumpolar region; it is evidently a postglacial relict. Interesting also are species like *Xysticus saganus*, whose closest relatives are found in North America, much as in *Antrodiaetus* and certain Opiliones. Only two (not three as stated) are Holarctic, namely, *Misumena vatia* and *Ozyptila sincera*.

All in all, the work is valuable, and the author is to be congratulated.

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Hammen, L. van der 1989. An Introduction to Comparative Arachnology. SPB Academic Publishing, The Hague. 576 pp. 302 figs. (Price \$150.00).

Progress in comparative arachnology suffers from the absence of an authoritative and accessible introductory text that outlines our current understanding of arachnid evolution, explains important controversies and suggests profitable avenues for research. Despite the promise of its title, van der Hammen's book is not an attempt to fill this vacuum. In fact, the author informs us at the outset that it is "not a handbook but a general survey of personal insights." It is primarily a review of van der Hammen's descriptive studies, and the author makes no real effort to summarize discoveries or opinions of other workers. Arachnologists familiar with van der Hammen's research will find little new information, but the book may serve as a reference for those requiring access to a summary of van der Hammen's contributions to arachnology.

The book is divided into two sections, a 70-page "general part" and a 500-page "systematic part". There is a list of references that includes most of the important work in comparative arachnology.

The general part summarizes basic aspects of arachnid biology, concentrating on areas of particular interest to systematists (external morphology, reproduction, postembryonic development and phylogeny), but there are no discussions of paleontology or biogeography. Van der Hammen gives little attention to internal

morphology or to arachnids as living organisms (i.e., behavior, functional morphology, ecology, physiology).

In his overview of arachnid morphology, van der Hammen summarizes the *Bauplan* of each order, concentrating on tagmata, mouthparts, appendages, coxal glands and genital structures. This section is not appropriate as an introduction to arachnid morphology, as van der Hammen assumes that the reader is already familiar with the higher arachnid taxa and presents his own controversial interpretations with an air of certainty generally reserved for time-tested hypotheses (e.g., "The problem of the homologization of leg segments is now definitely solved"). It is unlikely that a nonspecialist would be able to discriminate arachnological "facts" from van der Hammen's proposals. Throughout this summary the author uses an original system of terminology that he hopes will facilitate comparisons between arachnid orders, but he does a great disservice to himself and the reader by not including a glossary or index. Terms are sometimes defined parenthetically when introduced, but this is clearly inappropriate for what is basically a reference book that will not be read from cover-to-cover.

The section on postembryonic development outlines a general framework for the comparative study of arachnid life cycles. Acarologists are ahead of most other arachnologists in extracting information from development for use in systematics and for addressing general evolutionary topics, such as heterochrony. The issues van der Hammen addresses may inspire araneologists, scorpionologists, etc. to pay closer attention to preadult instars.

As van der Hammen is best known for championing the view that Acari is diphyletic and for his novel reconstructions of arachnid ordinal relationships, I had expected a more thorough treatment of these subjects within the section devoted to phylogeny. Here the author describes his latest phylogenetic hypothesis and outlines the characteristics of new superordinal taxa, but he does not provide the kind of explicit analysis that most systematists have come to expect. Although he occasionally uses the language of phylogenetic systematics, van der Hammen rejects cladistics as an "atomistic" methodology that leads to "highly artificial classifications". He favors a "structuralist" approach in which higher taxa are recognized by unexpressed potentialities ("deep structure") rather than their observable manifestations. In the absence of a more complete discussion of his methodology and its application to arachnids, van der Hammen's phylogenetic hypotheses are not convincing.

In the systematic part, van der Hammen describes the external morphology of one or two representatives from each of the generally recognized arachnid orders and major subordinal taxa, giving special attention to 'primitive' species. Each order is treated in a separate chapter, and chapter contents are organized to facilitate comparisons. In keeping with the author's specialty, over 300 pages are devoted to mites. His descriptions of several phylogenetically significant mite taxa (opilioacarines, holothyrids and a primitive actinedid) are especially thorough. Chapters dealing with the remaining arachnids and *Limulus* are either exact reproductions or slightly expanded versions of the author's four-part series "Comparative Studies in Chelicerata". These chapters contain some novel observations and insights, but it seems that their main purpose is to encompass nonacarines within the author's system of terminology rather than to make original contributions. The descriptions are accompanied by numerous well-executed line drawings.

Van der Hammen's comparative method has benefits and drawbacks. By providing intensive descriptions of primitive or "typical" representatives from each major group, he includes the basic morphology of each taxon as well as potentially significant minutiae that a more synthetic approach would omit. One has the satisfaction of being introduced to a real organism rather than a generalized cartoon. On the other hand, van der Hammen tends to get bogged down in details and leaves the task of critical synthesis largely to the reader. There is a tendency to gloss over variation within diverse groups, and little mention is made of phylogenetic relationships within orders.

In summary, the book is inappropriate as an introductory text. The author tends to ignore or trivialize research and opinions other than his own, and he frequently presents his untested proposals as accepted facts. In contrast, van der Hammen's talent for description and the phylogenetically significant taxa he includes make this a useful reference work for comparative arachnologists. The book's price will probably limit its distribution to libraries, but, as it is basically a review of van der Hammen's earlier work, most of the valuable information is available free of charge from the primary literature.

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Coddington, J. A. (Ed.). 1989. Spider literature: a computer bibliography, version 1.0. Available from the editor at the Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560 USA.

Arachnology, like many other endeavors, is being tremendously advanced by the application of affordable and approachable microcomputer technology. The bibliographic tool provided by this compilation is a superb case in point. Spiders, and collections of them, are myriad; the problems arachnologists face in dealing with tens of thousands of specimens and taxa are enormous. The difficulties added in dealing with an explosively enlarging literature are equally acute. Various aids exist, of course, including catalogs of taxa and indices of publications, such as the annual compilations provided by the Zoological Record and the Centre International de Documentation Arachnologique. Those aids suffer, however, from limitations imposed by the printed form in which they are distributed. Most notably, they individually cover limited time spans, and permit efficient searching through relatively few (and predefined) routes.

In this computerized bibliography, most of those limitations are overcome. This first public release includes over 11,000 citations to published papers, mostly from 1965 to date (although the complete bibliographies of Brignoli's catalog, extending back to 1940, as well as more recent supplements to it, are included). All post-1965 publications cited in the CIDA lists and all post-1977 publications cited in the Zoological Record (and many omitted by both those sources) are included. The bibliography is distributed in the form of ASCII files on floppy disks. It is most readily obtainable for MS-DOS systems, as the convenient IBM extended character set, including many frequently encountered accented

characters, is used. The files can easily be moved to other hardware systems, however, with special editing required only for those accented characters.

One could use these files as normal word-processing documents, and simply search repetitively for particular combinations of characters (names of authors, taxa, or places, for example). But they gain maximal utility when imported into modern database software, including text-based systems (such as AskSam, by Seaside Software), full relational databases (such as R:BASE, by Microrim), or specifically bibliographic software (such as Paperbase, by Wight Scientific). Importing the files usually requires minimal editing; for example, I was able to import the full 1.8 million characters into R:BASE in less than 30 minutes, using a powerful ASCII text editor (XyWrite III Plus, by XyQuest) to globally change the characters marking the ends of each field and record. As distributed, each reference includes three fields: one for the author(s) and year of publication, one for the title, and one for the journal reference (or publisher) and keywords (if available). Text-based software can absorb these fields directly; relational database software may require users to specify a maximum number of characters per field (which can waste much disk space), and deal individually with overly long entries. Some relational databases, such as R:BASE, have a field type that is flexible in size and can therefore handle all these references automatically, using minimal disk space. The files are in native Paperbase format, and that software (obtainable at a discounted price with the files) allows flexible output (in the formats specific to particular journals) as well as multiple string searches and easy file editing, indexing, and maintenance.

Once imported, one can easily obtain lists of all papers whose titles or keyword references include any string of characters. Thus, one has at one's fingertips citations to all papers that meet a specified criterion: all papers authored or coauthored by a given individual, for example (I've noted problems only in alternative transliterations of author's names from non-Roman—especially Russian—alphabets), or all papers whose titles or keywords include a given taxon name and/or geographic area (with allowances for linguistic differences, e.g., Brasil or Brazil), or all papers published in a given journal during specified years (here again, standardization of journal abbreviations is occasionally a problem).

Coddington has recruited an international coterie of collaborators who are hard at work extending the bibliography back in time (primarily through incorporating the bibliographies in Bonnet's catalog and similar sources), and annual updates are planned. The compilation and updating are far from simple processes; because of the variety of sources involved, discrepancies in format and duplications of titles require careful attention—byte by byte, character by character—to each entry. Persons wishing copies of the files can obtain them merely by agreeing to help with these efforts.

The usefulness of this database cannot be overestimated. To give just one example, I've recently been concerned with some kleptoparasitic spiders of the family Mysmenidae; by merely searching the title and keyword fields for all references that include the character string "klepto" I was able to find several important papers that might otherwise have been overlooked.

In short, Coddington has provided arachnologists with an enormously powerful tool that should do much to overcome the hazards of the modern "information explosion." That he has done so within an academic framework not yet prepared to reward such "electronic" publications is even more laudable. The advent of

such powerful handles on the literature makes it imperative that authors devote some effort to incorporating, in their titles, taxon names and keywords that will allow citations to be retrieved efficiently (hopefully, the days of "One Hundred New Species of Spiders" are long gone!).

Norman I. Platnick, American Museum of Natural History, New York, New York 10024 USA.

THE JOURNAL OF ARACHNOLOGY

Instructions to Authors

GENERAL COMMENTS

Manuscripts are acceptable in English, French, or Spanish, and must be **TYPED DOUBLE- OR TRIPLE-SPACED THROUGHOUT**. Good quality paper should be used and erasable bond is specifically excluded. Leave margins at least 1.5 in. (4 cm) on the left and 1 in. (2.5 cm) on the top, bottom, and right. Do not hyphenate any words at the right margin. Avoid using right justification in manuscripts prepared on word processors. Do not edit your own manuscript. *Italics* are permitted only to indicate scientific names; only the **TITLE**, **PRIMARY HEADINGS** (e.g., **INTRODUCTION**, etc.) and **RUNNING HEADS** should be typed in capital letters. Follow the recommendations of *Council of Biological Editors (CBE) Style Manual*, Third Edition, unless indicated otherwise below. To facilitate prompt review by two or more referees, send to the Associate Editor three identical copies of the typed material, one of which should be designated as the "original," together with copies of the illustrations.

Manuscripts longer than about 1500 words (five double-spaced typewritten pages in Elite, six double-spaced typewritten pages in Pica) should be prepared as Feature Articles, shorter papers as Research Notes. Manuscripts and all related correspondence must be sent to the Associate Editor: Dr. Jerome S. Rovner, Department of Zoological Sciences, Ohio University, Irvine Hall, Athens, Ohio 45701.

FEATURE ARTICLES

Arrange the various part of feature articles in the following sequence: (1) mailing address, (2) title, (3) by-line, (4) abstract, (5) body of text, (6) acknowledgments, (7) literature cited, (8) figure legends, (9) footnotes, (10) running head, (11) tables with legends, (12) figures. Put only parts 1, 2 and 3 on page 1, and start page 2 with part 4. All other pages are numbered consecutively.

Mailing address.—Include the complete address and telephone number of that author with whom all correspondence with the Editors should be handled.

Title.—When using common or scientific names in the title, be sure to include in parentheses the appropriate higher taxa (order, family, . . .). Include footnote indication if appropriate (e.g., to acknowledge grant support), but type footnote separately (see part 9 above). The title should be typed in capital letters and may not exceed 48 characters and spaces per line.

By-line.—Include the name(s) of author(s) as customarily written (less titles) and complete address(es), including zip code or other postal designation. Include footnote indication(s) if appropriate (e.g., to indicate change of address), but type footnote separately (see part 9 above). Leave three spaces between title and by-line, and four spaces between name(s) and address(es).

Abstract.—The abstract should be a summary of the basic findings, and should not exceed 2 to 3 percent of the text in length. Papers in a language other than English must be accompanied by an English abstract as well as an abstract in the language of the text. Papers written in English but focusing on a subject pertaining to a country where another of the accepted languages is used, may include an abstract in that language.

Body of text.—Use whatever form seems best to accommodate the necessary description of research. Be concise. Conform to standard references for abbreviations, i.e. the *CBE Style Manual* for scientific abbreviations, and a good language reference such as *The Little, Brown Handbook* for abbreviations of English words. Use the metric system for all measurements (the English system is acceptable only when transcribing locality data accompanying museum specimens), and note that abbreviations of metric units of measurements are not punctuated (e.g., mm and km, but ft. and mi.). Citations should be in the following form: Bellrose (1950); Bellrose (1950:33); or (Bellrose 1950). The complete scientific name of a species or genus, including author(s), must be given the first time they are mentioned in the text. Use single-line notation for fractions [e.g., 1/4 and not ¼; (4-12)/3 and not $\frac{4-12}{3}$].

The following special directions apply to authors of taxonomic papers:

(a). Do not use abbreviations in a primary heading to indicate that a new name or a new combination is being proposed (e.g., *A-us x-us*, **new species**, rather than *A-us x-us*, **n. sp.** or comparable abbreviations).

(b). Keys must be typed as follows:

1. Use Arabic numerals to designate the leading entry of the couplet.....2
Do not designate the second entry of a couplet, either by means of numbers, letters or other marks.....*A-us x-us*
2. Type numbers flush to left margin, and start entry on fifth space.....*A-us y-us*
Subsequent lines of any entry must also be indented five spaces.....*A-us z-us*

(c). Synonymies must follow the abbreviated style shown below:

A-us x-us Jones 1930:3, 1935:9; Russell 1945:453; Smith 1954a:16, 1954b:678; Cooper and Lim 1955:18 (in part).

A-us y-us Bates 1932:18, fig. 4. NEW SYNONYMY.

A-us z-us: Miranda 1948:98 (misidentification); Harris 1951:3 (in part?). (*nec A-us z-us* Zimmer).

(d). Lists of specimens examined of a given taxon must be the last items typed in the treatment of that taxon as they will be set in smaller type. Adhere to the following style for listing specimens examined: Country: State or comparable political subdivision; County or District, detailed locality (elevation), 14 July 1945 (collector): 2 males, 5 females (acronym of institution where specimens are deposited), next detailed locality within that County, etc.; next County in the same State; etc.: next State in the same Country: etc. Next Country: etc. Punctuation rules are very simple. Use a period to separate countries, a colon to separate states, a semi-colon to separate counties, and a comma to separate specific localities.

Acknowledgments.—Avoid overlooking persons who have in some substantial way assisted with the work. Authors of taxonomic papers should spell out the name and indicate parenthetically the acronym of institutions where specimens studied are deposited, if not mentioned elsewhere in the text.

Literature Cited.—Include only those publications to which reference is made in the text. Adhere to the *CBE Style Manual* and refer to a previous issue of The Journal of Arachnology for style. Do not abbreviate place names in journal citations. Repeat name(s) of author(s) in case of multiple entries.

Figure Legends.—Provide one legend for each illustration which will be reproduced separately, or for each "plate" consisting of several illustrations. Adhere to the following styles:

Figs. 1-4.—*A-us x-us*, male from Timbuktu: 1, left leg; 2, right chelicera; 3, dorsale aspect of genitalia; 4, ventral aspect of abdomen.

Figs. 27-34.—Right chelicerae of species of *A-us* from Timbuktu: Figs. 27, 29, 31, 33.—Dorsal views; Figs. 28, 30, 32, 34.—Prolateral views of movable finger; Figs. 27-28: *A-us x-us*, holotype male; Figs. 29-30: *A-us w-us*, male; Figs. 31-32: *A-us z-us*, holotype male; Figs. 33-34: *A-us t-us*, male. Scale = 1.0 mm.

Type all figure legends consecutively on the same page(s), double spacing lines within each legend and leaving 4 spaces between legends. Keep in mind that 99 characters and spaces represent one printed line, and that 4 mm for each printed line must be subtracted from the maximum height permissible on full-page illustrations.

Footnotes.—Footnotes will be permitted on page 1 when it is appropriate to acknowledge grant support and to indicate change of address, etc. No footnotes will be permitted on any other page. Type footnotes together on a separate page.

Running head.—At the top of each right hand page will be printed the author(s)' last name(s) and an abbreviated title. This running head may not exceed 60 characters and spaces, must be typed in capital letters, and a hyphen must separate the name(s) from the title.

Tables with legends.—Prepare all tables precisely as they are to be typeset. Construct tables as simply as possible. Include the legend at the top of each. Make marginal notations in the text which clearly indicate the appropriate point of insertion of each table. Note that in these instructions "graphs" are regarded as "figures," not "tables."

The size of the printed page imposes a limit on the size of tables that can be accepted. In a normal, upright table these limits are 99 characters and spaces per line and 56 lines in height, including legend. Sideways tables are difficult to typeset and present problems during paste-up; therefore, they will be accepted in exceptional cases only, as most tables that are "too wide" can usually be rearranged to fit into the more desirable, upright position. Any table that exceeds the dimensions given above will not be accepted for publication. Tables must be typed double-spaced throughout, and the legend must be in the following style:

Table 1.—Incorporate into the legend all information necessary to make the data presented clearly understandable. Do not use footnotes.

Figures.—Figures are the only parts of the paper for which the author is responsible for preparation of camera-ready material, and therefore they must be executed with great care. Drawings should be made with black drawing ink on high quality, smooth, white, heavy paper. Drawings made in some manner not employing black ink (e.g., shaded pencil drawings) are difficult to print, more so than photographs. When such a technique is used, the drawings should be fairly dark, have good contrast, and be well executed. The largest dimensions on the printed page on which illustrative material (with legends) will be printed is 127 by 200 mm. Decisions as to size of originals, placement of several smaller drawings on a single page, etc., should be based upon this format. Where several smaller drawings are to appear together on a single page, it is the responsibility of the author(s) to furnish an assembled “plate” precisely as it should appear in print. An effort should be made to efficiently utilize the available space within the limits of the original “plate.” The “plate” must be prepared to allow for inclusion of the legend beneath the drawings on the same printed page. Number all drawings consecutively using Arabic numerals; do not designate illustrations with letters, and never designate plates. Labeling should be neat, secure, and done with a method which produces flat characters, e.g., pressure-sensitive transfer characters or a lettering apparatus employing black ink. Photographs should have good contrast, be glossy or semi-glossy, and printed slightly larger (up to 2X) than anticipated published size. Photographs and inked drawings should not be grouped together in a single plate, because they will be difficult to print. ***Illustrative material of any kind larger than two times the anticipated printed size will not be accepted.*** Larger illustrations are difficult to handle and are easily damaged or lost in the mail. Authors preparing larger illustrations should consult local photo shops and print firms about the availability of PMT's (PhotoMechanical Transfer) for reducing their illustrations to an acceptable size. PMT's are high contrast, direct positive-to-positive reproductions on semi-glossy paper, which will also give the author(s) a good idea of how the illustrations will look when printed. PMT's can be obtained at a reasonable cost in a number of sizes, usually 8 by 10 in. or 9 by 12 in., with any amount of figure reduction desired within that space. Sending PMT's rather than originals avoids the loss of art work in the mail, and if the PMT's get lost or damaged they can be replaced. Illustrations, PMT's, and photographs must be securely mounted on stiff white paper or mounting board (Scotch Magic Transparent Tape can be used on the white portions of illustration paper). On the back of each plate include author's name(s), abbreviated title of manuscript (or running head), figure numbers included, and orientation (= topside). Illustrative material that is poorly prepared, too large, or not mounted properly will be returned to the author.

RESEARCH NOTES

Arrange the various parts of your research notes in the following sequence: (1) mailing address, (2) title, (3) body of text, (4) by-line, (5) figure legends, tables with legends, and illustrations. Follow instructions given above for feature articles unless otherwise indicated below. Do not include footnotes anywhere. References to grant support and all other acknowledgments should be made in a statement in the body of the text. If an indication of change of address is desired, it should be included parenthetically after the credited institution as “present address.” For citation of literature, follow the same instructions as for Feature Articles. The by-line must be typed in paragraph form after the body of the text or the literature cited when one is present. When possible, Research Notes will take priority over Feature Articles in the publication sequence.

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Membership in the Society is open to all persons interested in the Arachnida. Annual dues are \$30.00 for regular members, \$20.00 for student members and \$50.00 for institutions. Correspondence concerning membership in the Society must be addressed to the Membership Secretary. Members of the Society receive a subscription to *The Journal of Arachnology*. In addition, members receive the biannual newsletter of the Society, *American Arachnology*.

American Arachnology, edited by the Secretary, contains arachnological news and comments, requests for specimens and hard-to-find literature, information about arachnology courses and professional meetings, abstracts of papers presented at the Society's meetings, address changes and new listings of subscribers, and many other items intended to keep arachnologists informed about recent events and developments in arachnology. Contributions for *American Arachnology* must be sent directly to the Secretary of the Society.

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